index + plates DEC 8 1919

Vol. 11, Nos. 3 and 4 October, 1919

PARASITOLOGY

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CAMBRIDGE UNIVERSITY PRESS
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LONDON: FETTER LANE, E.C. 4
ALSO
H. K. LEWIS AND CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
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Cambridge University Press, Fetter Lane, London, E.C. 4

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VOLUME XI OCTOBER, 1919 NOS. 3 AND 4

INTESTINAL PROTOZOA FOUND DURING ACUTE INTESTINAL CONDITIONS AMONGST MEMBERS OF THE EGYPTIAN EXPEDITIONARY FORCE, 1916—1917.

BY F. W. O'CONNOR, M.R.C.S., D.T.M. AND H. (CAMB.),
(Temp.) CAPTAIN, R.A.M.C.
London School of Tropical Medicine.

(With Plate XI and 3 Text-figures.)

[A REPORT TO THE MEDICAL RESEARCH COMMITTEE.]

IN the summer of 1916, during the advance across Sinai, the prevalence of amoebic dysentery amongst our troops occasioned the appointment of a Protozoologist to the Field Laboratories. While I was engaged in this capacity the work recorded in this paper was carried out.

Investigations were made in several laboratories and I am indebted to the several bacteriologists who co-operated in this work; especially to Major A. R. Ferguson, R.A.M.C., who organized and controlled the laboratories, and Captains C. M. Craig, R.A.M.C., and G. Stuart, R.A.M.C., T.F., with whom I worked for many months. Captain Linklater, R.A.M.C., T.F., and the late Captain Ian MacFarlane, R.A.M.C., rendered me valuable assistance in collecting clinical data of many cases. Lieut.-Col. P. Lelean, C.B., R.A.M.C., helped me materially by organizing the collection of specimens from all units, many of which were many miles distant from the laboratory. I am very much indebted to Col. A. Alcock, F.R.S., and Prof. Clifford Dobell, F.R.S., for the help they have given me in preparing this paper for publication.

According to instructions all stools from diarrhoeal cases were examined twice for the cholera vibrio by the bacteriologists, and by myself as often as was necessary—sometimes six times—for *Entamoeba histolytica* and other Protozoa. Where possible, as in units in the immediate vicinity, the whole stool was inspected. From units at a distance specimens were sent in specially-made glass or tin tubes, tightly corked.

The cases included white troops, Indian native troops, and members of the Egyptian Labour Corps. During periods of advance when the laboratory was left behind for a short time and the amount of routine work in consequence

diminished, I examined a series of supposed healthy Egyptian labourers with a view to ascertaining the percentage of *Entamoeba histolytica* carriers in this large co-operating force.

The number of cases examined, with the macro- and microscopical appearances of the stools and the number of cases in which the different Protozoa were found, together with the percentages of each, are given for each month in the appended tables.

After the laboratories had been established for some time all specimens arrived fresh and were therefore easily examined. At first the following difficulties were encountered.

1. Specimens collected over night and sent to the laboratory next day arrived stale; free Protozoa were generally dead or degenerated and could not be identified. Orders were circulated that only material passed on the day of transmission should be sent and that transport should be as rapid as possible.

2. Specimens were sent in which the cell-elements were dead or degenerated owing to:

(*a*) The stools having been passed into pans along with the urine. Urine bottles were therefore provided and instructions issued for the passage of urine and faeces into separate utensils.

(*b*) Pans being used which contained, or had recently been cleaned with, antiseptics. Orders were issued that stools from which samples were required should only be passed into pans containing no antiseptics, or which, after antiseptic treatment, had been thoroughly washed and dried.

3. *Admixture of sand with specimens.* This was difficult to overcome. As it rendered the adjustment of cover-slips necessary for fine focus impossible, attendants were requested to see that receptacles had tight-fitting covers, which were to be removed only immediately before use, and to be replaced immediately afterwards. Patients also were provided with toilet paper and they were advised against letting it come in contact with the desert sand.

Methods of Examination.

When present in a specimen, blood and mucus and faecal material were always examined.

Films were studied by the method used by Wenyon in London, and Wenyon and the writer in Alexandria, but when I discovered that Protozoa could be seen as small shiny dots with the $\frac{2}{3}''$ objective, I always—before using the $\frac{1}{6}''$ and $\frac{1}{12}''$—made a rapid preliminary examination of three preparations with the $\frac{2}{3}''$, and by this means I recognized many scanty infections that otherwise might, I think, have been overlooked. When using the $\frac{2}{3}''$ objective one learns with a little practice to differentiate between Protozoa and small vegetable organisms which at first appear like protozoal cysts.

Character of the Stools.

A careful record was made of the appearance and consistency of each specimen examined and the results are shown in the appended tables. Free Protozoa were generally found in stools containing blood, mucus, etc., and in those of a liquid character, and cysts in the more solid faeces of a later stage. In semi-solid stools both free and encysted Protozoa were found, and these were the most satisfactory to examine. In cases passing hard formed stools I generally gave the patient half an ounce of magnesium sulphate 2-hourly, until the first soft motion was passed for examination, in preference to large single doses of this salt or other purges.

Blood and Mucus Stools.

This condition was found in association with bacillary or amoebic dysentery and in some of the native cases caused by *Schistosoma mansoni* or *haematobium*. By far the greater proportion of cases was bacillary in origin.

In the Acute Bacillary cases in the earliest stages the dejecta consisted of almost pure blood, or more frequently of thin watery or slightly tenacious mucus brightly stained with blood. Sometimes the mucus was more viscid, streaked or tinged with blood. In other cases faecal material was stained with streaks of blood and approached to the amoebic type. Very occasionally a complete absence of blood on naked eye inspection and a preponderance of liquid mucus made one suspicious of cholera; but this appearance was more frequently observed in the few cases of ptomaine or food poisoning which occurred from time to time. Stools continued in these conditions for from 24 hours to a week and then, with decrease of the red corpuscles and increase of pus and epithelial elements resulting in a preponderance of mucus, merged into a liquid form of bacillary stool to be described under "Liquid Stools."

In Amoebic Dysentery the classical type of stool, faecal in character with streaks and spots of blood-stained mucus, predominated, but in a few cases large infections of active phagocytic amoeba were found where the macroscopic appearance suggested the bacillary disease. Bacteriological investigation in these cases failed to reveal a bacillary cause, and rapid improvement followed treatment with emetine. In one case a "Rice Water" stool sent for examination for the cholera vibrio contained large numbers of free amoebae cytologically identical with *Entamoeba histolytica* but containing no red blood cells; the comma bacillus was not found, and the following day the patient passed faeces containing many amoebae loaded with red cells, and the diagnosis of amoebic dysentery was confirmed.

In the one case of simultaneous amoebic and bacillary dysentery the naked eye appearance suggested the latter disease.

In dysenteric conditions due to *Schistosoma* the stool generally consisted of almost pure unaltered blood. Though this appearance was the most common one yet in other cases the character varied from the typical to any of those described for bacillary or amoebic dysentery.

Liquid Stools.

The macroscopical appearance of diarrhoeal stools caused by some of the dysenteries in the latter stages and also by the less pathogenic organisms are subject to great variation. Three types recently observed, however, are worth mentioning.

In *Lamblia* infections the stools may be any colour or consistency during the encysted stage of the organism and the same applies where small numbers of the free flagellate are being passed; but when the free flagellate appears to be causing diarrhoea a yellow ochreous motion with streaks or pin point dots of mucus without blood is fairly constant. I have noticed similarly coloured stools with other conditions. Nevertheless when such stools were associated with mucus, *Lamblia* was generally present.

During the latter stages of bacillary dysentery a yellow liquid stool smelling very offensively is frequently encountered; it is often seen without blood and mucus and in patients who have recently passed through a bad attack of bacillary dysentery.

Sometimes one meets with a grey or brownish-grey liquid stool. The history generally given is that the patient felt a griping pain in the stomach. This was followed by desire to defaecate and the act was accompanied by a distressing scalding sensation in the anal canal and round the external sphincter, which persisted for some time after the act of defaecation was completed. In these cases two or three such stools may be passed daily and the condition, if untreated, may persist for two or three days, then passing away gradually. If treated with a one ounce dose of magnesium sulphate it disappears within 24 hours. In stools from these cases I have almost invariably found one or other of the vegetable organisms to be described presently. I encountered 15 cases of this kind.

The naked eye appearances therefore of dysenteric stools are of considerable value in guiding one as to the causative organism of an acute diarrhoeal condition, but no confident diagnosis can be based on this form of examination alone, owing to the great variation of type even in one disease, and the tendency of one type to merge into that of another.

MICROSCOPICAL EXAMINATIONS.

Dysenteric Stools. In the very early acute stages of bacillary dysentery the red blood cell element generally predominates, the white cells being fewer in proportion. This stage is rarely seen by the laboratory worker as it generally announces the beginning of the attack, is transient, and rapidly gives place to the next and most commonly seen phase, where white cells very soon increase numerically and cause the red cells to appear more scanty. In typical cases there is a marked degeneration of the epithelial and leucocyte cells passed, as was pointed out by Bahr (*Dysentery in Fiji*). But in the earlier stages degeneration is not so marked, and moreover, as sometimes a similar degeneration of cells is noticeable in amoebic cases, and in the cells cast off in bilharzia

dysentery, a positive diagnosis of bacillary dysentery from the microscopical appearance of the cell-element alone can only be considered unscientific. Although in bacillary dysentery the cell element is generally greater in amount than is the case in the amoebic disease, yet this is not invariably the case (see Case H).

In amoebic cases the microscopical findings vary according to the portion of the specimen examined. In blood and mucus, red blood corpuscles predominate as a rule, although I have found amoebae containing these red cells moving in a medium of degenerated leucocytes and epithelial cells and when bacteriological control failed to reveal evidence of double infection. The amount of cell-exudate and its character bears some relation to the extent of bowel affected and to the acuteness of the particular attack.

In *Lamblia* cases even when the free flagellate is present and is matted together in large numbers, the cell element is conspicuous by its absence.

In the foul liquid motions following acute bacillary dysentery, leucocytes and epithelial cells in an advanced state of degeneration equivalent to pus, with little or no admixture of red cells, is a common feature.

Cells are not generally found in the cases associated with fungi.

AMOEBIC DYSENTERY.

Observations on the parasite of this disease were made from examinations of 88 acute cases. Cases were considered acute when red blood cells were found within active amoebae.

In none of the cases was the temperature raised above 99° F. Most of the cases gave a history of recurrent attacks of diarrhoea at long intervals dating back to the Gallipoli campaign. Five only could be said with reasonable certainty to have originated on the Sinai Desert. Cases showing rectal symptoms associated with tenesmus, pain, and tenderness in the region of the descending colon predominated over those complaining of griping before stool and tenderness in the caecal region.

An account of one case will demonstrate the insidious onset and the subacute course of the disease, with mild symptoms which are sometimes out of all proportion to the wholesale destruction of large intestine which may be taking place. It will also clearly show the reason for some of the observations made in this paper:

Case Pte. W. H. Admitted to Casualty Clearing Station in a state of collapse, 18. ix. 16.

Past History. Patient never left England before the war, and gave no history of previous serious illness. He arrived in Egypt direct from home on January 19th, 1916. After spending two nights in Alexandria with his draft he proceeded to the Sinai Desert, where he had served since.

History of Present Condition. Towards the end of April 1916 patient went sick, complaining of diarrhoea and abdominal pain, principally before defaecation, though tenesmus accompanied the act. He was treated in a Field Ambulance for a fortnight and then given light duty for a week. He then returned to full duty; from that time onwards he occasionally had two or three motions a day and latterly his comrades remarked that he was getting thin.

He did not report sick and took his place on the march with the other men. For three weeks before admission, becoming weak, he was posted to duty as batman. Motions had now become numerous but he continued on duty. Three days before admission he had to fall out on the march through weakness and diarrhoea and he then noticed some blood in his motions. He was treated for two days at the Regimental Aid Post and then, as he was becoming steadily weaker, he was admitted to the Casualty Clearing Station.

Condition on Admission. Patient was in a very much collapsed condition. Face thin and shrunken. Tongue coated and dry. Pulse rapid and easily compressible. Temperature 97° F. Abdomen hard and movements restricted; generally tender and resistant to palpation. The liver dulness was not increased. Ten to twelve motions occurred daily, the material passed being thin and watery with flakes of mucus and epithelial tissue and sometimes a little blood in streaks. The general condition suggested cholera, and a specimen was sent to the laboratory for examination. Owing to the long distance between the Casualty Clearing Station and the laboratory the specimen did not arrive for 15 hours.

Microscopical Examination. Large numbers of degenerated leucocytes and epithelial cells, and other large cells which might have been either amoebae or tissue cells were seen. No definite amoebae were observed. In these circumstances, and as the comma bacillus was not isolated, a provisional diagnosis of bacillary dysentery was given, and a request for an early and fresher specimen was made. The patient, however, rapidly sank and died next morning. A partial autopsy was made, and the liver, spleen and the large intestine were sent by horse to the laboratory. The tissues, which were still warm on arrival, were examined by Major A. R. Ferguson, R.A.M.C., and myself.

The *liver* was engorged and on section dark, sanguineous fluid flowed out; its texture was soft; it was not much enlarged. No abscesses were found.

The *spleen* was slightly enlarged and congested.

The *large intestine.* From the ileo-caecal valve to just above the anal canal the intestine was in a state of advanced ulceration. Only two islands of apparently healthy tissue, each about the size of a five-shilling piece, were left. The epithelial lining was almost completely destroyed. In many places the submucous coat was extensively ulcerated; in one spot a perforation of the peritoneum was seen, but this probably occurred during post mortem manipulation as there was no evidence of general peritonitis. The attached mesenteric glands were matted together, enlarged and hard, but suppuration had not taken place. Material was examined microscopically from the bases of some of the ulcers. Considerable numbers of large phagocytic amoebae were found, many of them containing red blood cells. The movements of these amoebae were sluggish and consisted in the protrusion of long fine tapering processes (Text-fig. 1). This kind of movement was evident in some sixty individuals examined, and differed markedly from the sudden bursting and rolling movements seen in amoebae passed in the stools of patients suffering from the disease. The nucleus was in every instance *E. histolytica* in type. Although several experimental cultures were made, both from the specimen of the stool and from the tissue sent after death, no specific bacillary infection was discovered.

The following points are worth noting in this case:

1. The very insidious onset and the subacute course of the disease.

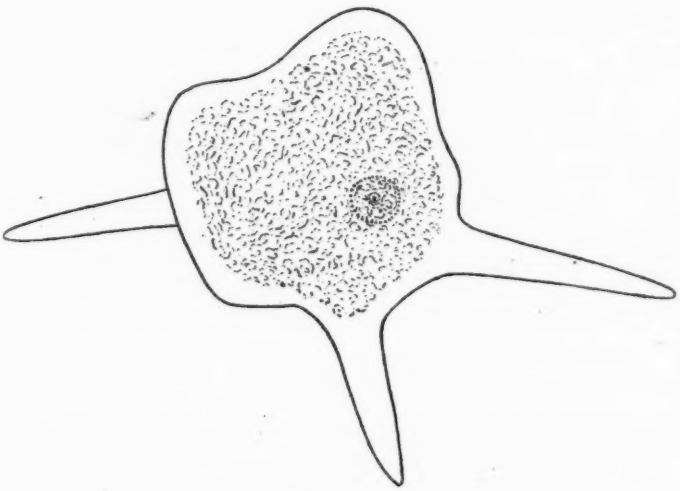
2. The extensive destruction of large intestine co-existent with the patient's ability and willingness to carry on his duties, always especially strenuous on the desert.

3. The almost sudden collapse which preceded the fatal termination of the disease, suggesting the possibility of cholera.

4. The ambiguity in diagnosis, owing to the rapid degeneration of cell-constituents in a stale stool in a hot climate.

5. The peculiar nature of the movements of the phagocytic amoebae taken from the fresh tissue.

In another case (Captain D.), the onset of the attack was sudden, although there was a history of attacks of diarrhoea in the past. In this case there was also an extensive cell exudate, but a few amoebae containing red blood cells were found on the first examination. *B. shiga* was subsequently isolated from this stool, the cell exudate being probably due to the action of the bacillus. Had a diagnosis been made on macroscopical characters, or on the nature of the exudate alone, the treatment of an active amoebic condition would have been neglected.



Text-fig. 1

THE PARASITE.

Entamoeba histolytica was discovered in 156 cases, or 7·5 per cent. of the white troops examined, but in only 50 cases was it found in the large free actively-motile phase, containing red blood cells, and associated with a clinical dysenteric condition. The parasite was found most frequently amongst the native Egyptian cases, and in these too the number of cases suffering from amoebic dysentery was also higher. Among the Indian native troops no cases of actual amoebic dysentery were found, but the number of these troops examined was very small.

The *Nucleus* of the amoebae in fresh specimens conformed to the *E. histolytica* type, although in specimens not quite fresh and occasionally at the edges of the slides examined, of the fresher cases, the other abnormal

types of nucleus were seen, in the sluggish, or non-motile amoebae. In specimens stained by the Heidenhain haematoxylin method from all classes of cases the atypical forms of nucleus predominated, the *E. histolytica* type of nucleus being very rarely found.

I am inclined to believe that the so-called "tetragena" nucleus of the free forms is due to a degenerative change caused by a contraction of the nucleus and a running together of the chromatin dots into clumps. The change can apparently take place very suddenly, since it was found in specimens fixed by the rapid wet-fixation method of corrosive sublimate and alcohol in cases which were on examination of fresh specimens obviously *E. histolytica*.

The so-called "minuta" forms have frequently been seen containing two nuclei and several were observed in my series, but I have seen for the first time in Case W., who was suffering from acute amoebic dysentery, considerable numbers of amoebae containing red blood cells and at the same time possessing two nuclei.

Throughout all the examinations only one case of simultaneous double acute amoebic and bacillary dysentery was observed: this was in the Case D. referred to in which *Bacillus dysenteriae* of Shiga was isolated. The bacilli of dysentery were found three times in cases harbouring *Entamoeba histolytica* cysts. *B. shiga* twice, and *B. flexner Y* once, but in these cases the protozoon appeared to have no effect on the patient's condition at the time.

It may be stated here that free and encysted intestinal protozoa were frequently found in the stools from which pathogenic bacteria were isolated. The presence of the latter appears to exercise no influence on the intestinal protozoa.

Entamoeba coli.

This parasite was found most frequently amongst Indian troops, and then, in order, in healthy Egyptians, sick Egyptians, and white troops. I observed no evidence of the pathogenicity of this parasite in the 923 cases in which I encountered it. It was demonstrated by Wenyon and myself in 1916 that when faeces containing *Entamoeba coli* were mixed with fresh blood and kept warm in the laboratory, the blood cells tended to run together around the amoeba and adhere to it, but that in no case were they seen inside the parasite: further it was noticed that the amoeba did not try to ingest the cells. During my examination of the above cases, including a number of *Schistosoma* infections where the patients were passing almost pure blood in which *Entamoeba coli* were found, I have observed the same phenomenon.

The Inclusions of Entamoeba coli.

Foreign bodies of various kinds, including protozoa, have been reported by many observers as being found in free *E. coli*. In my examinations the following inclusions were found:

Entamoeba histolytica cysts	Twice
Lamblia cysts	Twice
Free *Lamblia*, non-motile and apparently dead ...	Once
Chilomastix cysts	Once
Vegetable cells resembling *Chilomastix* cysts ...	Once
Isospora hominis oocysts	Once

In one of the cases of *Lamblia* inclusions, no less than 30 different amoebae were found to have taken up one or more cysts: in many of these two cysts were included, in a few three, and in one degenerated parasite, in which, however, the outlines of cell and nucleus could still be made out, there were five. In stained specimens from this case I have found many amoebae with two *Lamblia* cysts included. In the fresh state, amoebae, containing many cysts, were motile and apparently healthy. In several instances, however, although the cell was motile, the nucleus was large and faint with small masses of chromatin distributed round the edge and throughout its interior.

The case of *Isospora* inclusions was especially interesting. Captain McLean, R.A.M.C., sent me the specimen as a case of Coccidiosis for confirmation of his diagnosis. The oocysts developed in three days to the state typical of Isospora, viz., two sporocysts, each containing four sporozoites and residual body. As the infection was a heavy one, I asked Captain McLean to send me specimens daily in order that I might follow the case. This he very kindly arranged to do. The patient also had a large infection of *Entamoeba coli*. On the third examination I discovered an oocyst rolling on the slide like a Rugby football on its long axis, and on closer examination I observed a motile amoeba stretched over it, the nucleus of the amoeba being quite clear and typically *E. coli* in appearance; the rolling over movement of the oocyst was obviously due to the movements of the investing amoeba, and the latter was apparently unaffected by the enormous inclusion. On further examination I found more than ten amoebae with similar inclusions. I made several Heidenhain haematoxylin preparations and I was fortunate in getting some well stained specimens in which, although the contents of the oocysts cannot be made out, yet the walls and contour of the *Isospora* are clearly demonstrable within the amoeba.

When free protozoa are ingested by free *Entamoeba coli* it seems reasonable to assume that the former may be digested. In the case of the free *Lamblia* which I found in one *E. coli* the flagellate was non-motile and granular. But in the case of inclusion of the highly resistant protozoal cysts the effect on the amoeba or on its inclusion is not so easily explained. As I have already stated, I have seen *Isospora* oocysts and *Lamblia* cysts in actively motile *E. coli* which were apparently in no way affected by such inclusions. In one *Lamblia* case the nuclei of the investing amoebae had undergone change in spite of non-interference with the motility of the parasite: the nuclei in these amoebae were enlarged, spherical, and faintly outlined; the blocks of chromatin

around the periphery and the karyosome itself were broken up into minute dots, which were distributed irregularly around the nuclear edge and throughout the interior. In one amoeba containing five *Lamblia* cysts the host was non-motile and granular and the presence of a degenerated nucleus and the shrunken protoplasm gave the clue to the diagnosis of *Entamoeba coli*. In this case the amoeba seemed to have died of repletion owing to the size and number of the inclusions. In no case did the ingested protozoal cysts seem to be affected by their confinement. In one *Lamblia* case the eosin, which on application stained a dead amoeba, did not penetrate or stain a *Lamblia* cyst included in the amoeba.

Although chromatoid bodies have been known to occur in *Entamoeba coli* cysts, nevertheless these bodies have generally been considered to be of uncommon occurrence in the non-pathogenic amoeba. I made careful examinations in 293 cases of *E. coli* infection to see in how many cases I could find "chromidial bodies." I found the body present in some of the cysts in 15 out of 110 white cases and in 17 out of 183 healthy Egyptian cases, or in 32 out of 293 altogether. The bodies were generally more slender than those found in *E. histolytica* cysts and often appeared as pointed spindles; the big "chromidial blocks" so common in the latter infection were not found, except in some of the binucleate *E. coli* cysts: even when present in *Entamoeba coli* cysts, chromatoid bodies were very rarely seen in such great numbers of cysts as in *E. histolytica* infections: two cases in which these bodies were present in *E. coli* cysts in large numbers were found in Alexandria (Wenyon and O'Connor). I found only one similar case during the Sinai examinations.

Trichomonas hominis.

Tetratrichomonas was the form in which this parasite was most frequently seen, although *Trichomonas* (sensu stricto) was not uncommonly found.

In three cases of *Trichomonas* infection complicated by the passage of blood and mucus in the faeces, red blood cells were observed within the flagellate. Two of these cases were Indian soldiers and the other was a native Egyptian. In each case many of the Trichomonads included a corpuscle, but only one red cell was observed in any particular parasite. As these findings lent support to the view sometimes advanced that *Trichomonas* is pathogenic, I arranged to have my cases carefully controlled bacteriologically by Captain G. Stuart, R.A.M.C., T.F. This officer isolated Flexner Y from one case, and in another a non-lactose fermenting organism was found, which, however, failed to agglutinate with any of the known sera. The third case from which no organism was isolated, occurred in a native Egyptian who was passing large masses of *Schistosoma mansoni* in a medium of red blood, pus and epithelial cells. *Schistosoma* was obviously the cause of the man's condition. A number of other cases associated with the presence of *Trichomonas*, but in which blood and mucus were not passed, were also controlled bacteriologically, and in many of these a definite pathogenic bacillus was isolated. Species of

Trichomonas are very common among the rodents of the desert. The gerbille and the jerboa as well as small mice were found to be almost invariably infected with it. I examined over 30 of these animals where although Trichomonads were not found in the hard pellet-like faeces of the rectum, they were generally discovered in considerable numbers in the soft contents of the caecum and ascending colon. In none of the rodents examined did I find evidence of invasion of the epithelial lining of the intestine or of even superficial ulceration of that tissue.

Lamblia intestinalis.

I have been so frequently questioned as to the importance of this parasite, as a cause of symptoms or disease, that it might serve some useful purpose if I give my opinion, which is based on the examination of a large number of cases. In all excepting three of the cases investigated by me the patients showed little or no evidence of inconvenience as the result of harbouring the parasite.

In the three cases referred to the patients suffered from neurasthenia. They stated they experienced a sense of fulness in the abdomen above the umbilicus, with a frequent desire to go to stool, and periodical attacks of diarrhoea: occasionally a sensation of nausea was complained of, but this did not result in vomiting. These symptoms in a less degree were complained of by other patients, but the latter made light of it and maintained that it neither inconvenienced them considerably nor prevented them from doing their work. In no case, even in those who suffered from diarrhoea associated with the passage of the free flagellate uncomplicated by other conditions, did I find either tissue or blood cells or other evidence of a morbid process. The free forms of the parasite were generally present in a medium of mucus without cells. Occasionally the parasite was passed in enormous numbers and the amount of mucus was then considerable. When this occurs in individuals who are run down, by overwork or by the effects of climate, there is a tendency for patients first to become interested in their stools and then to become imbued with the idea that they are suffering from a serious disease. I have always been most careful to consult the clinician when I have found *Lamblia* in a case and to point out that the parasite should only be considered of importance when present in debilitated individuals. I think it is a mistake to put a diagnosis of "*Lamblia intestinalis*" on the Medical History Sheets where patients can see it. Many patients have said to me, "I am suffering from Lamblia dysentery, Sir, and the Doctor says that there is no cure for it."

"*Entamoeba*" *nana.*

This parasite was found in 112 of the white cases, 32 of the Egyptian sick, 14 of the Indian sick, and only 27 times amongst the healthy Egyptians (the small number in the last series being due no doubt to the fact that only single examinations were made). As in the case of the other "Entamoebae"

the organism occurred most frequently in the encysted state. I observed no evidence of its pathogenicity.

When once an individual becomes infected with this parasite apparently he remains so for a long time. I have at present one case under observation who still has the infection after two years. This patient was first known to harbour the parasite shortly after it was named. Many of my cases have been controlled on culture to obviate the possibility of missing small free living amoebae of the limax group, which it so closely resembles. In none of my cases did a growth take place on agar.

Tricercomonas.

Owing to the minuteness of this parasite and to the difficulty, in consequence, of making out its essential points, namely the flattened side with attached flagellum passing beyond the tail prolongation, it is possible that I missed some infections and that the figures given by me do not represent the full numbers of infections which occurred in the series. The cystic stage described as occurring once in the Alexandria examinations was not met with at all amongst the desert cases. The flagellate was observed about 16 times for all cases examined on the desert.

Coccidiosis. Isospora hominis.

The oocysts of Isospora were found in nine cases. Of these seven occurred in white troops, one in Indian troops and one in the sick Egyptians. *Eimeria* was not seen. Diagnosis was only made on examination of fully developed cysts containing sporocysts with sporozoites. This development took place in from 24 to 48 hours after the passage of the stool. In warm weather cysts showing sporocysts were generally found within 24 hours of defaecation. The greatest number of mature cysts in all seasons were found after three days. A considerable number of the cysts degenerated without forming sporocysts. In these cysts the protoplasm of the sporoblast became swollen and finely granular, the nucleus disappeared and greenish oily looking globules appeared in the interior: with time the globules replaced the other elements, which disappeared. Degeneration usually took place in the sporoblast stage and before sporocyst formation had commenced.

Two very heavy infections with this organism were observed. In one, Case S., the patient, a new recruit, said that he had not been out of England until January 1916. He was then sent to Alexandria and at once proceeded to the desert. He was amongst a guard placed at an Out Station where flies were a pest. Four weeks later he experienced dull pain in the epigastrium and right hypochondrium, and he had a feeling of nausea which became worse after food. Patient was well nourished, tongue slightly coated, abdomen distended with flatus. On palpation no swelling was felt, but there was slight tenderness at the lower edge of the liver on the right side. The patient was treated with Emetine Hydrochloride gr. 1 hypodermically for 12 days.

Throughout the treatment and for three weeks afterwards, during which patient was carefully observed, there was no change in the physical condition or in the number of oocysts passed.

Case R. This patient was the one in whose stools the oocysts were found in the *Entamoeba coli*. Although he passed even more oocysts than Case S. yet he complained of no symptoms which could be attributed to the parasite.

I therefore have no conclusive evidence to prove that *Isospora* is or is not pathogenic.

Animal Experiments with Isospora.

An attempt was made to infect two new-born puppies with *Isospora* from Case S. The puppies were placed within a few hours after birth in a fly-proof cage about ten feet above the ground and they were milk-fed through a pipette. When one month old Puppy A was given two teaspoonfuls of well macerated faeces in which there were numerous fully developed oocysts. Milk was used as a medium. The stools, which were normal, were frequently examined and no parasites were found. The puppy remained well for three weeks. On the 21st day after the administration of the dose, evidence of weakness of the hind legs was noticeable, and towards the end of the same day efforts to maintain the erect position completely failed. The abdomen was very much distended and respiratory distress became marked. Next morning as the distress was very great the animal was chloroformed. Some liquid motions had been passed for two days before death; cells were found in these, but none resembling the schizonts or oocysts of Coccidia. On post mortem examination the large and small intestines were found distended with flatus. The first two inches of the small gut were markedly hyperaemic and there was a quantity of mucus in this part of the bowel; a few hyperaemic patches were also seen in the caecum; the glands in the omentum were swollen and soft; the liver, spleen and lungs showed no evidence of disease. Microscopical examination of the mucus and of the intestine and liver, fixed at the time of the autopsy and subsequently stained, showed no evidence of coccidial infection. Haemorrhages were found in the submucosa of the intestine and extending up the centre of the intestinal villi. The glands were found to have undergone advanced fatty degeneration.

Puppy B infected a week after Puppy A died after 23 days under exactly similar circumstances. Post mortem examination showed the same changes as in Puppy A. No evidence of coccidial infection was found in either case.

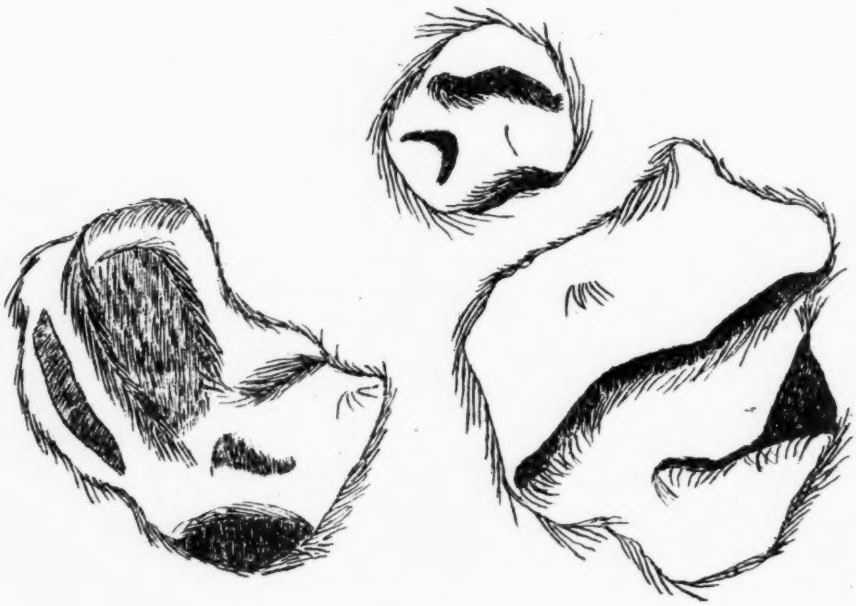
Vegetable Cells found associated with Diarrhoea.

Whenever vegetable cells were found apparently causing diarrhoea, the appearance of the stools and the symptoms complained of were fairly constant.

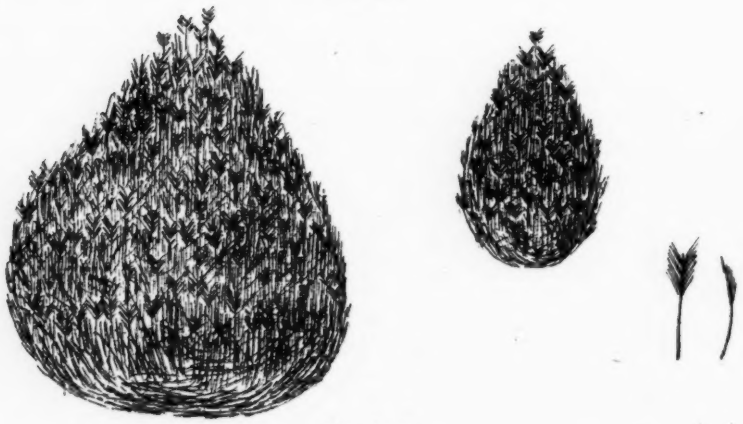
The cells found were:

1. Blastocysts in various forms.
2. Vegetable organisms resembling *Chilomastix* cysts.
3. "I cysts."

4. (Text-fig. 2.) A shiny greenish body varying from a few microns to such a size as almost to fill a field under the $\frac{1}{12}''$ objective. This cell, which had no uniform shape, was invariably covered sparsely with rough simple



Text-fig. 2



Text-fig. 3

hair-like projections which tended to recurve at the point. There was no evidence of a nucleus, and on preservation no further development of the cells was observed to take place.

5. (Text-fig. 3.) A flask-shaped brown body varying from 12–60 μ in its long axis, thickly covered with compound hairs generally growing in the same direction to the top of the cell, where they became concentrated and formed a rough projection.

The first three vegetable cells mentioned were only occasionally noticed to be associated with diarrhoea; they then occurred in large numbers. Whenever found, the cells described as 4 and 5 were invariably accompanied by the form of diarrhoea described earlier, and of the two kinds of cells the first was the more common.

The vegetable structures resembling *Chilomastix* cysts were often discovered in many men about the same time. On one occasion I found them in 15 different patients of the same battalion in two days. I have never found them associated with diarrhoea which could be attributed to their presence.

Vegetable cells have been so frequently reported in the stools of patients suffering from diarrhoea in warm countries, and I have found them so frequently in similar cases for which no cause could be discovered, that I think it is highly desirable that mycologists should devote their attention to these and other fungi in human stools.

DESCRIPTION OF PLATE XI.

Figs. 1, 2. Pathogenic entamoebae containing red blood cells and showing, in Fig. 1, the *E. histolytica* type of nucleus and, in Fig. 2, the so-called *tetragena* type of nucleus; both amoebae occurring in the same slide. (Case Pte. S. 5. xii. 16.)

Fig. 3. Pathogenic entamoeba with red blood cells included and showing two nuclei in the parasite. (Case W. 21. i. 17.)

Figs. 4–7. *Entamoeba coli*. Free forms. Showing various protozoal and vegetable cell inclusions. Fig. 4. A much vacuolated amoeba, with characteristic nucleus and containing a uninucleate *E. histolytica* cyst; "chromidia" can be seen within the cyst. (Case C. 30. iii. 17.)

Figs. 5 and 6. Amoebae containing *Lamblia* cysts. The nucleus in these amoebae is atypical, being enlarged, faintly defined and with the chromatin granules much split up. The case was controlled for several days and in the cystic phase only *E. coli* cysts were passed. The latter were mostly 8-nuclear. (Case W. S. 11. xi. 16.)

Fig. 7. *Entamoeba coli* from another case showing *Lamblia* cyst included. The nucleus here is characteristically *E. coli*. (Case A. 1. vi. 17.)

Fig. 8. *Entamoeba coli* with included vegetable cells resembling *Chilomastix* cysts. From same case as Fig. 7.

Figs. 9, 10. Two *Entamoeba coli*, each showing included an oocyst of *Isospora*. In Fig. 9 the oocyst is lying along its long axis and the stretching of the amoeba at the poles of the cyst can be seen. In Fig. 10 an optical section of the oocyst in its narrow axis is shown: in this figure the remains of the shrunken and degenerated protoplasm can be made out. In both cysts the double contour of the cyst wall can be observed in part of its extent. (Case R. 14 vi. 17.)

Fig. 11. Characteristic appearance of *Entamoeba coli* as seen in a medium of almost pure blood from a case of *Schistosoma mansoni* causing dysenteric symptoms. The tendency of the red cells to collect around and adhere to the parasite is seen. No red cells are present in the interior of the amoeba. (Native Egyptian, Case 227, 5. v. 17.)

Table I. *Stools examined and findings in White Troops, suffering from Dysenteric or Diarrhoeal Conditions.*

	No. of cases examined	No. of cases containing Blood and Mucus	No. of cases containing Mucus without Blood	No. of Liquid Stools	No. containing Red Blood, Pus and Epithelial Cells	No. of *Entamoeba histolytica*	*Entamoeba histolytica* %	*Entamoeba histolytica* Free	*Entamoeba histolytica* Cysts	*Entamoeba histolytica minuta*	*Entamoeba histolytica minuta* Cysts	*Entamoeba coli*	*Entamoeba coli* %	*Entamoeba coli* Free	*Entamoeba coli* Cysts	*Entamoeba nana*	*Entamoeba nana* %	*Entamoeba nana* Free	*Entamoeba nana* Cysts	*Lamblia intestinalis*	*Lamblia intestinalis* %	*Lamblia intestinalis* Free	*Lamblia intestinalis* Cysts	*Chilomastix mesnili*	*Chilomastix mesnili* %	*Chilomastix mesnili* Free	*Chilomastix mesnili* Cysts	*Trichomonas hominis*	*Trichomonas hominis* %	*Tricercomonas*	*Tricercomonas* %	*Isospora hominis*	*Isospora hominis* %
1916																																	
Aug.	14	1	—	3	2	1	7	—		1	3	21·4			3																		
Sept.	338	79	15	85	103	29	8·5	10	4	15	69	20·4	23	46	13	3·8	6	7	29	1	7	1	7	1								
Oct.	315	62	24	40	96	38	12	16	3	19	97	30·8	29	68	25	8	—	25	28	8·9	5	23	30	9·5	30	—	18	5·7	2	0·6	2	0·6
Nov.	134	19	11	19	43	8	6	3	—	5	28	21	6	22	9	6·7	—	9	4	3	1	3	5	3·7	5	—	5	3·7			1	0·7
Dec.	168	27	17	19	61	10	6	2	—	8	44	26	13	31	7	4	1	6	1	0·6	—	1	3	1·8	2	1	5	3				
1917																																
Jan.	190	21	20	46	57	21	11	6	1	14	46	24	8	38	8	4·2	—	8	14	7·4	—	14	6	3·2	6	—	7	3·7				
Feb.	94	8	5	26	15	9	9·5	3	1	5	27	28·5	6	21	7	7·4	4	3	15	16	1	14	4	4·2	4	0	9	9·5	1	1·1		
March	65	12	9	10	26	6	9·2	2	2	2	8	12·3	5	3	4	6·1	2	2	2	3	—	2	1	1·5	—	1	1	1·5				
April	138	10	13	17	15	7	5	—	1	6	36	26	6	30	15	10·8	2	13	9	6·5	1	8	2	1·5	2	—	5	3·7				
May	226	15	21	36	59	6	2·6	1	1	4	46	20·3	12	34	8	3·5	—	8	16	7	—	16	5	2·2	1	4	2	0·9				
June	161	36	9	24	62	11	6·8	4	3	4	37	23	14	23	11	6·8	6	5	14	8·7	2	12	10	6·2	9	1	1	0·6	3	1·8	2	1·2
July	199	38	14	43	92	8	4	3	1	4	30	15	9	21	4	2	—	4	16	8	1	15	10	5	8	2	5	2·5				
Aug.	40	4	3	7	12	2	5	—	—	2	7	17·5	2	5	1	2·5	—	1	7	17·5	—	7	3	7·5	2	1	1	2·5	1	2·5	—	
Totals	2082	332	161	375	643	156	7·5	50	17	89	478	23	133	345	112	5·4	21	91	156	7·5	11	145	107	5·1	96	11	66	3·2	7	0·3	7	0·3

Table II. *Stools examined and findings in Members of the Egyptian Labour Corps, suffering from Dysenteric or Diarrhoeal Conditions.*

	No. of cases examined	No. of cases containing Blood and Mucus	No. of cases containing Mucus without Blood	No. of Liquid Stools	No. containing Red Blood, Pus and Epithelial Cells	No. of *Entamoeba histolytica*	*Entamoeba histolytica* %	*Entamoeba histolytica* Free	*Entamoeba histolytica* Cysts	*Entamoeba histolytica minuta*	*Entamoeba histolytica minuta* Cysts	*Entamoeba coli*	*Entamoeba coli* %	*Entamoeba coli* Free	*Entamoeba coli* Cysts	*Entamoeba nana*	*Entamoeba nana* %	*Entamoeba nana* Free	*Entamoeba nana* Cysts	*Lamblia intestinalis*	*Lamblia intestinalis* %	*Lamblia intestinalis* Free	*Lamblia intestinalis* Cysts	*Chilomastix mesnili*	*Chilomastix mesnili* %	*Chilomastix mesnili* Free	*Chilomastix mesnili* Cysts	*Trichomonas hominis*	*Trichomonas hominis* %	*Tricercomonas*	*Tricercomonas* %	*Isospora hominis*	*Isospora hominis* %
1916																																	
Sept.	23	9	1	4	13	5	21·7	4	—	1	2	8·7	2																				
Oct.	98	15	6	7	20	12	12·2	6	1	5	19	19·4	6	13	2	2·04	—	2	4	4·1	—	4	1	1	1	—	4	4·1				
Nov.	37	18	6	4	21	4	10·8	4	—	—	7	18·9	5	2													1	2·7				
Dec.	19	12	4	3	18	2	10·5	2	—	—	2	10·5	2																				
1917																																	
Jan.	7	1	1	3	4	1	14·3	1	—	—	1	14·3	—	1																			
April	17	8	4	1	13	3	17·65	1	—	2	3	17·6	2	1																			
May	194	33	22	38	68	9	4·6	7	—	2	40	20·6	18	22	7	3·1	1	6	9	4·6		9	6	3·1	5	1	10	5·1				
June	168	32	22	10	70	23	13·7	8	2	13	56	33·3	19	37	15	8·9	6	9	9	5·4		9	15	8·9	14	1	9	5·3	4	2·4		
July	104	16	11	7	32	11	10·6	5	—	6	42	40·4	17	25	8	7·7	5	3	5	4·8		5	7	6·7	7	—	5	4·8	2	1·9	1	0·9
Totals	667	144	77	77	259	70	10·49	38	3	29	172	25·8	71	101	32	4·8	12	20	27	4·05	—	27	30	4·5	27	3	32	4·8	6	0·9	1	0·15

Table III. *Stools examined and findings in Indian (Native) Troops, suffering from Dysenteric or Diarrhoeal Conditions.*

1917	No. of cases examined	No. of cases containing Blood and Mucus	No. of cases containing Mucus without Blood	No. of Liquid Stools	No. containing Red Blood, Pus and Epithelial Cells	No. of *Entamoeba histolytica*	*Entamoeba histolytica* %	*Entamoeba histolytica* Free	*Entamoeba histolytica minuta*	*Entamoeba histolytica* Cysts	*Entamoeba coli*	*Entamoeba coli* %	*Entamoeba coli* Free	*Entamoeba coli* Cysts	*Entamoeba nana*	*Entamoeba nana* %	*Entamoeba nana* Free	*Entamoeba nana* Cysts	*Lamblia intestinalis*	*Lamblia intestinalis* %	*Lamblia intestinalis* Free	*Lamblia intestinalis* Cysts	*Chilomastix mesnili*	*Chilomastix mesnili* %	*Chilomastix mesnili* Free	*Chilomastix mesnili* Cysts	*Trichomonas hominis*	*Trichomonas hominis* %	*Tricercomonas*	*Tricercomonas* %	*Isospora hominis*	*Isospora hominis* %
March	2	—	2	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	50	—	—	—	—
April	23	5	3	1	8	3	13	—	—	3	4	17·4	1	3	6	26·1	2	4	1	4·3	—	1	5	22·6	5	—	3	13	2	8·7	—	—
May	63	5	6	14	17	10	15·9	—	—	10	22	34·9	1	21	5	7·9	—	5	2	3·2	—	—	2	5	7·9	3	2	7	11·1	—	—	1	1·6
June	11	2	2	3	5	1	9·1	—	—	1	4	36·4	2	2	3	27·3	1	2	—	—	—	—	2	5	18·2	2	—	1	9·1	1	9·1	—	—
Totals	99	12	13	18	32	14	14·1	—	—	14	30	30·3	4	26	14	14·1	3	11	3	3·03	—	3	12	12·1	10	2	12	12·1	3	3·03	1	1·03

Table IV. *Stools examined and findings in Members of the Egyptian Labour Corps, doing ordinary duty at the time, and not complaining of illness*.*

No. of cases examined	*Entamoeba histolytica*	*Entamoeba histolytica* %	*Entamoeba coli*	*Entamoeba coli* %	*Entamoeba nana*	*Entamoeba nana* %	*Lamblia intestinalis*	*Lamblia intestinalis* %	*Chilomastix mesnili*	*Chilomastix mesnili* %	*Trichomonas hominis*	*Trichomonas hominis* %	*Tricercomonas*	*Tricercomonas* %	*Isospora hominis*	*Isospora hominis* %
1006	73	7·25	243	24·2	27	2·7	34	3·4	14	1·4	5	0·5	3	0·3	—	—

* Observations of Helminthic ova found during examinations have been made. These will be considered in a subsequent paper.

THE GENUS *LERNAEOPODA*.

INCLUDING A DESCRIPTION OF *L. MUSTELICOLA* N.SP., REMARKS ON *L. GALEI* AND FURTHER OBSERVATIONS ON *L. SCYLLICOLA*.

By W. HAROLD LEIGH-SHARPE, B.Sc. (Lond.)

(With 7 Text-figures.)

The four commonest species of *Lernaeopoda* likely to be met with in British waters are:

L. SCYLLICOLA **Leigh-Sharpe** 1915	*Parasitology* VIII, 262[1] and XI, 18[1].
L. GALEI **Krøyer** 1837	
L. GLOBOSA **Leigh-Sharpe** 1918	*Parasitology* XI, 29[1].
L. MUSTELICOLA **N.sp.** 1919	(*desuper*).

L. MUSTELICOLA[2] N.SP.

Habitat and Record. Two specimens, ♀, were taken on *Mustelus vulgaris* ♂, the smooth hound, captured at Plymouth in August 1918. They were attached in the angle between the host's body and the pelvic fin and slightly to the left. [This location is unfortunate since the length of the attaching "arms" (2nd maxillae) I have endeavoured elsewhere to show, is a variable character not to be depended upon for the determination of species; for it is my experience that *Lernaeopoda* spp. have arms very short in this location.]

Body. The general form is best understood by reference to Fig. 1 D.

Dimensions. Length of: cephalothorax 2 mm.; trunk over 4 mm.; ovisacs 4 mm.; abdominal appendages 1 mm.; second maxillae 2·5 mm. (but may depend upon location).

Cephalothorax. Differs but slightly from that of other species in respect to form, but shows black pigmentation anteriorly and round the edges, no such pigmentation occurring in other species hitherto described.

Trunk. Slender, even narrower anteriorly than in *L. scyllicola*, without postero-dorsal protrusion, not compressed postero-laterally.

[1] See these papers for references herein quoted.

[2] Not to be confused with *L. musteli* Thomson (1889) occurring on *Mustelus antarcticus* in the vicinity of New Zealand.

Abdominal Appendages. Unusually small ($\frac{1}{6}$th of body-length), situated ventrally to ovisacs as in the rest of the genus.

Appendages (Fig. 2). According with those of other species, but the spines and processes thereon but few, basal portion of first maxillae larger, second maxillae, or "arms," noticeably short, less than half the length of the trunk, swollen basally. The bulla injured, but more concave and proportionately broader than in *L. scyllicola*. The mandibles (Fig. 3 D) resembling those of *L. galei*, under which heading they are discussed, but having a spherical base which bears a prominent hooked projection on the inner border. The maxillipedes (Fig. 4 D) are described in the comparison on p. 261.

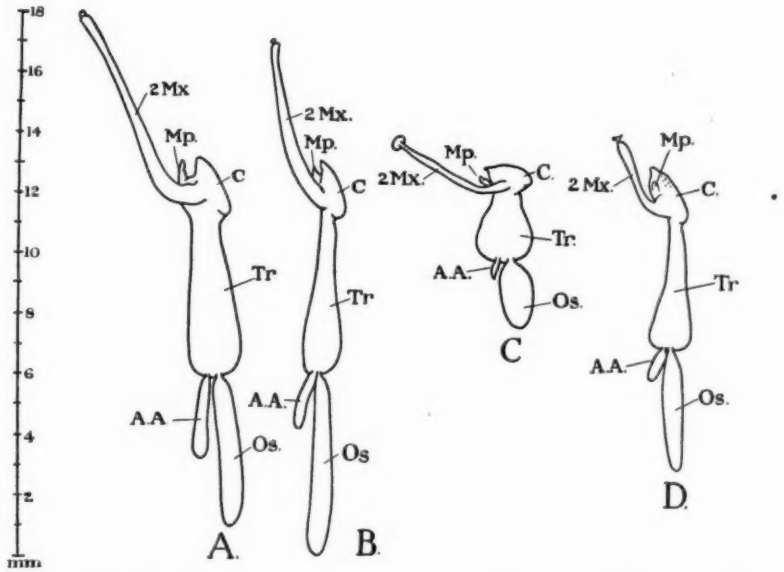


Fig. 1. A comparative scheme of the four commonest species of *Lernaeopoda* ♀ in profile: **A.** *L. scyllicola*; **B.** *L. galei*; **C.** *L. globosa*; **D.** *L. mustelicola*. *c.* cephalothorax; *Tr.* trunk; *2Mx.* 2nd maxillae ("arms"); *Mp.* maxillipedes; *Os.* ovisacs; *A.A.* abdominal appendages. Compare (1) the contour of cephalothorax, the angle of its inclination to the trunk, and the degree of its dorsiventral compression; (2) the contour of trunk; (3) the posture of "arms."

Generic Characters (female). See *Parasitology*, VIII, 272.

Specific Characters (female). Cephalothorax pigmented with black dots. Proximal end of second maxillae swollen. Ovisacs short (4 mm., about $\frac{2}{3}$ length of trunk). Abdominal appendages short (1 mm. about $\frac{1}{6}$ length of trunk). The base of the mandible bears a hooked projection on the inner side. Basal joint of the maxillipede with three cushions of spines arranged in a ternate manner, the two upper side by side, the lower one close below them without any spine or hook between.

L. GALEI.

Habitat and Record. Two specimens, ♀, were taken on *Galeus vulgaris* ♂, the tope, captured at Plymouth in August 1918. They were attached between the claspers in the extra-cloacal region.

Body. *Vide* Fig. 1 B.

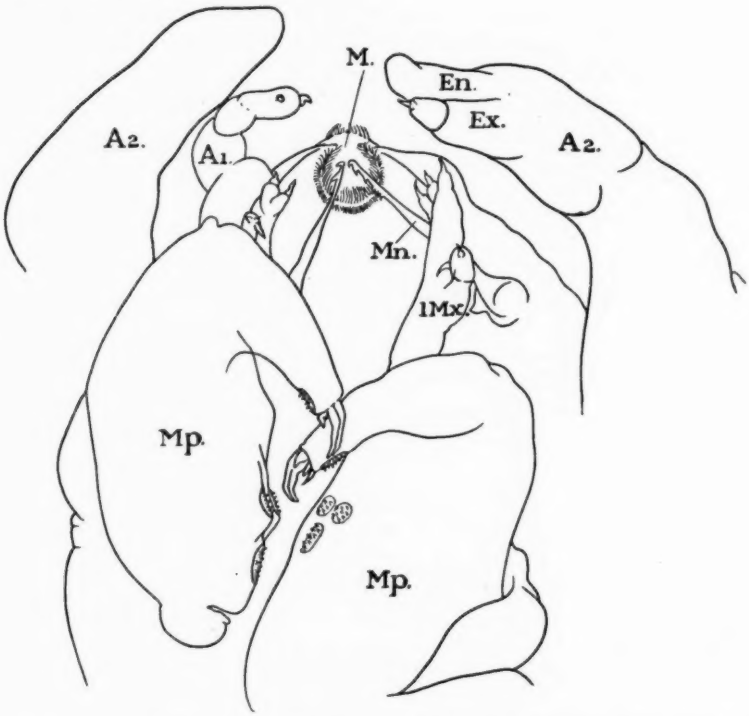


Fig. 2. *Lernaeopoda mustelicola.* The anterior end of the female in ventral aspect showing some of the appendages *in situ*. *M.* mouth; *A1*, antennules; *A2*, antennae; *Mn.* mandibles; *1Mx.* 1st maxillae; *Mp.* maxillipedes; *Ex.* exopodite; *En.* endopodite.

Dimensions: compared with those of Wilson ("Parasitic Copepods of N. America").

	Leigh-Sharpe	Wilson
Length of cephalothorax	1·75 mm.	1·5 mm.
„ trunk	7	9
„ 2nd maxillae	5·5	4
„ abdominal appendages	nearly 2	2
„ ovisacs	6	10

From inspection of this table, were the dimensions of my specimens consistently smaller, one would expect that they were not fully grown.

Indeed I have seen in museums specimens alleged to be *L. galei*, far exceeding these in size.

Again in the ovisacs there are more eggs in a row than in *L. scyllicola*, viz. 29 or 30, as compared with 22 to 23 in the latter species. The individual ova are smaller than in *L. scyllicola*.

The only **appendages** of specific value are the mandibles and the maxillipedes:

The *mandibles* (Fig. 3 B) were very accurately described by Kurz, who distinguished three kinds of teeth: (1) principal teeth (Hauptzähne), much the largest, hatchet-like, usually curving backwards and alternating with (2) intermediate teeth (Zwischenzähne), which are very minute, serrate, triangular in shape, and occupy the base of the angles between the principal

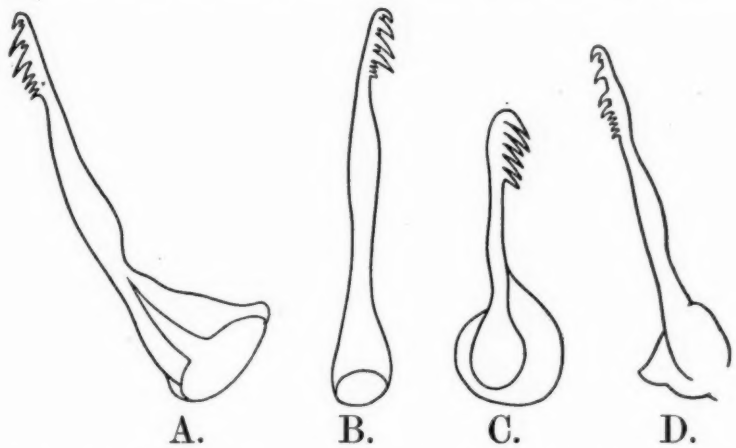


Fig. 3. A comparative scheme of the mandibles of the four commonest species of *Lernaeopoda* ♀. **A.** *L. scyllicola*; **B.** *L. galei*; **C.** *L. globosa*; **D.** *L. mustelicola*.

teeth; (3) secondary teeth (Nebenzähne), which follow in a continuous sequence behind the principal teeth diminishing regularly in size towards the proximal end of the mandible. In *L. galei* there are: one principal tooth (terminal), an intermediate tooth; three principal teeth with two intermediate teeth respectively between them, one between each; three secondary teeth.

The *maxillipedes* (Fig. 4 B) in my estimation, do not agree with the figures of Scott and Scott very closely. They consist of a basal joint which I should not describe as stout but only moderately so, and a terminal joint, not very powerful, terminating in a curved claw smaller than in other species, having at its base an accessory claw which is not ventral as in other species, but is situated on a lateral projection, as figured by Scott and Scott, who have (possibly intentionally) exaggerated it, and two smaller spines at the base on the side of the concavity. The terminal joint has the usual cushion

of spines not at all clearly defined, the teeth of which appear to grade into a general roughness of the cuticle which is distributed over the joint. The basal joint not only has the two usual cushions of spines on its inner side, but is provided with three other cushions, which, as far as I know, have escaped the notice of other investigators, one on the outer edge of the proximal end, one on the outer edge of the distal end and the third a very large spinous area where the appendage joins the body. Of the usual cushions on the inner margin, the more distal one opposes a rounded cushion of spines whose exact locality is still uncertain, but which appears to be situated on the animal's body, on peculiarly shaped ridges provided for the purpose; the proximal cushion is situated on a projecting boss at the extreme base of the joint, an unusual location not found in the other species, so that it very effectively opposes and in action touches its partner. There is no spine or hook between the cushions on the inner margin as in *L. scyllicola*.

* * * * *

The following table contains a comparison between the four common species of *Lernaeopoda* ♀ (*vide* Fig. 1).

Species	L. Scyllicola	L. Galei	L. Globosa	L. Mustelicola
Host	*Scyllium canicula*	*Galeus vulgaris*	*Scyllium canicula*	*Mustelus vulgaris*
Location	Extra-cloacal region, pelvic fins and claspers	Extra-cloacal region, pelvic fins and claspers	Nasal fossae	Pelvic region
Occurrence	On practically every male dogfish	Common	Fairly common	(? Common)
Length of:				
(1) Cephalothorax	**2** mm.	Over **1·5** mm.	Nearly **2** mm.	**2** mm.
(2) Trunk	5+2=**7** mm.	**7** to 9 mm.	1 (Head ⊥r to trunk) + over 2–**3** mm.	2+4=**6** mm.
Ratio of (1) to (2) ...	$\frac{2}{7}$	$\frac{2}{11}$	$\frac{2}{3}$	$\frac{1}{3}$
(3) 2nd maxillae (arms) ... (a variable character)	**7** mm.	**4** to **5·5** mm.	**4** mm.	**2·5** mm.
Ratio of (3) to (2) ...	1	$\frac{11}{14}$	$\frac{3}{4}$	$\frac{5}{12}$
(4) Ovisacs	**5** to 7 mm.	**6** to 10 mm.	Over 2 mm.	**4** mm.
Ratio of (4) to (2) ...	$\frac{5}{7}$ =(nearly)	$\frac{6}{7}$ =(nearly)	=(nearly)	$\frac{2}{3}$
(5) Abdominal appendages	**3** mm.	Nearly **2** mm.	**0·5** mm.	**1** mm.
Ratio of (5) to (2) ...	$\frac{3}{7}$	$\frac{2}{7}$	$\frac{1}{4}$	$\frac{1}{6}$
Ova: Rows	**4** to 6	**4** to 6	6 to 8	4
No. in a row ...	22 to 23	29 to 30	12	18
Bulla	Large, stud-like	Moderately large, stud-like	Small, the second maxillae also ending in two expanded discs	Moderately large, stud-like

The point of attachment of *Lernaeopoda* spp. upon the host in its bearing on the consequent length of the "arms" (second maxillae).

Species	Host	Location	Length of "arms"
L. elongata	*Lamna cornubica*	Eyes	20 mm. (longer than the trunk)*.
L. globosa	*Scyllium canicula*	Nasal fossae	4 mm. ($\frac{3}{4}$ length of trunk) but this is a *very* small species

Species	Host	Location	Length of "arms"
L. scyllicola	*S. canicula*	High up in the extra-cloacal aperture†	7 mm. (equal in length to trunk)
,,	,,	Clasper groove‡	3–5 mm.
,,	,,	Tip of clasper	1·5–2 mm.
L. scyllicola and *L. mustelicola*	,, *Mustelus vulgaris*	Above pelvic fins; between them and body wall	2·5 mm.

* I have not yet met with this species upon *Lamna*. My hypothesis, that those species having free play are short armed, is not supported in this instance.

† *Parasitology*, VIII, 263, Fig. 1, Position *a*.

‡ *ibid.* Fig. 1, Position *G*.

A comparison of the mandibles of the four commonest species of *Lernaeopoda* ♀ (Fig. 3).

(For a detailed discussion see under *L. galei*.)

Abbreviations: H, principal teeth; **Z,** intermediate teeth; **N,** secondary teeth.

L. SCYLLICOLA	L. GALEI	L. GLOBOSA	L. MUSTELICOLA
Heterodont The principal are serrate	Heterodont The principal are serrate	Homodont, all principal, uncinate, decrease in size proximally	Heterodont The principal are serrate
Formula:	*Formula:*	*Formula:*	*Formula:*
H1	H1	H6	H1
Z1	Z1	—	Z1
H1	H1	—	H1
Z1	Z1	—	H1
H1	H1	—	Z1
N4	Z1	—	H1
—	H1	—	N4
—	N3	—	—
Base: Somewhat triangular and flattened	*Base:* Spherical and small	*Base:* Spherical and of moderate size, somewhat flattened	*Base:* Spherical with a hooked projection on the inner side

A comparison of the maxillipedes of the four commonest species of *Lernaeopoda* ♀ (Fig. 4).

L. scyllicola. Basal joint long and slender, provided with two rounded cushions, well developed and covered with papillated spines. Proximal cushion situate at some distance anteriorly to base of joint. Between the cushions is a large mamillated, upwardly curved hook.

Terminal joint long and slender, provided with a rounded cushion of papillated spines also well-developed, and terminating in a long abruptly-curved claw, with an accessory claw at its base ventrally, and two smaller claws at the base, on the side of the concavity.

L. galei. Basal joint not long and slender, but somewhat stout, provided with two rounded cushions covered with papillated spines. Proximal cushion large, protruding as a boss at base of joint. *No* hook or spine between the cushions.

Terminal joint slender, provided with a rounded cushion of papillated spines, and terminating in a short curved claw with an accessory claw at its base which projects more than in other species, and two smaller claws at the base on the side of the concavity. I consider that the basal joint bears accessory cushions of spines at its proximal end which are not figured by other authors.

L. globosa. Basal joint not slender, provided with two small rounded cushions covered with feebly-developed spines. Near, but distal to the proximal cushion a poorly developed spine. Cushions are widely separated.

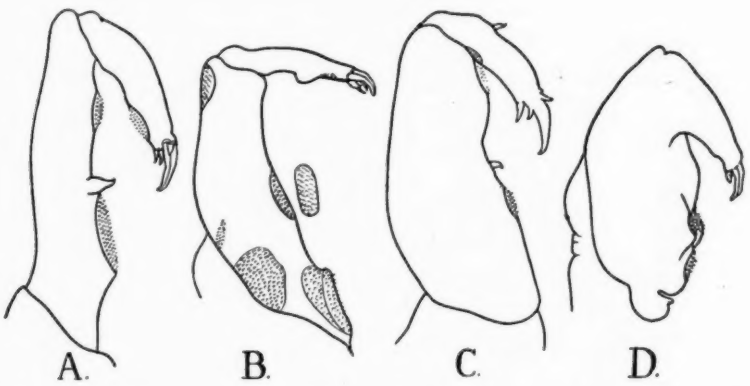


Fig. 4. A comparative scheme of the maxillipedes of the four commonest species of *Lernaeopoda* ♀. **A.** *L. scyllicola*; **B.** *L. galei*; **C.** *L. globosa*; **D.** *L. mustelicola.*

Terminal joint slender, provided with a small rounded cushion with poorly developed spines and terminating in a long abruptly-curved claw, with two accessory claws at its base on the inner side and one on the outer side. A characteristic small spine is also present on the outer side of the base of the joint.

L. mustelicola. Basal joint fairly stout provided with three cushions of papillated spines arranged in a ternate manner, the two more distal ones, situated side by side, probably corresponding to a single cushion in other species. Cushions close together and without spine or hook between them.

Terminal joint fairly stout, provided with a rounded cushion of papillated spines at the extreme end of its inner margin; and terminating in a curved claw with an accessory claw at its base ventrally and two smaller claws at the base on the side of the concavity.

L. SCYLLICOLA.

PART III.

Abnormal Growths. During the spring months of 1918, I observed upon *L. scyllicola* various abnormal spherical growths in different situations upon the cephalothorax, and the anterior portion of the trunk, notably the shoulder (Fig. 5). Under the low power of the microscope fine threads were seen

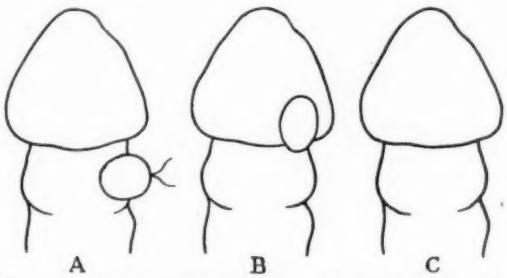


Fig. 5. *L. scyllicola*, some abnormal growths: **A.** on the shoulder; **B.** on the cephalothorax; **C.** normal outline.

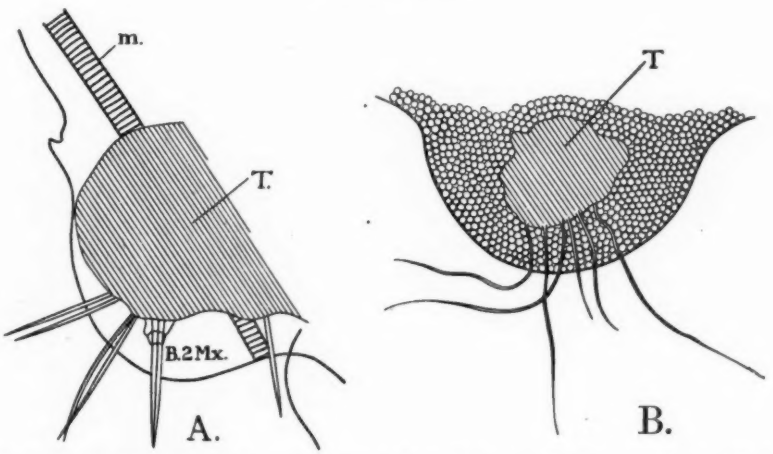


Fig. 6. Some abnormal growths or tumours under a high magnification. **A.** *L. mustelicola*; **B.** *L. scyllicola* (a microscopic enlargement of Fig. 5 A.). *T.* tumour; *m.* muscle; *B2Mx.* base of the second maxilla.

protruding from these growths. Upon the base of one of the second maxillae, and somewhat between them, of one of the specimens of *L. mustelicola* previously described (*vide ante*) a similar growth is present, in which the projecting threads are much stouter and straighter (Fig. 6 A). In a permanently mounted eosin-stained preparation under a $\frac{1}{8}$th-inch objective these growths resolve themselves into a solid mass of tissue embedded among the round

oily-looking tissue cells, which make up the body of the host, from which the filamentous processes arise, and penetrate the cuticle projecting far beyond the surface of the animal. The central mass of the growth does not exhibit any structure, neither do the tapering filaments. The growths may have arisen from abrasions or wounds caused by the embrace of the male, the filaments possibly represent a vegetable growth that gained entrance to the wound.

The Bulla. Since studying *Clavella* (*Parasitology*, XI, 120, fig. 4) it appears to me that what I have called the bulla in *Lernaeopoda* (*Parasitology*, VIII, 268, fig. 4 A) corresponds only to the manubrium ("pedicel" of Wilson) of *Clavella*, and that possibly a cylindrical mass of tissue which fits into the saucer-like concavity of the upper portion of the strongly-chitinised organ in *Lernaeopoda*, which I have hitherto regarded as part of the host (wound-healing tissue), is the real bulla (homologous with the structure so called by me in *Clavella*), derived from the frontal filament, while the manubrium is derived from the second maxillae. I fail to discover from Wilson's text whether he bears out this view, and his figures of *Lernaeopoda* afford no explanation. His figures of enormous bullae in *Salmincola* (e.g. *S. inermis* with a bulla as large as the whole animal) seem to confirm my opinion. This mass of tissue is very slightly chitinised if at all, is vague in shape, possesses no markings, and is easily parted from the manubrial portion, so that it is almost invariably left behind in the host.

Antennal Organs. Michael G. L. Perkins, whilst working with me, found that on staining the female with methylene blue and afterwards washing out with 90 per cent. alcohol all the stain was removed from the whole animal except from five spots in the antenna. These are indicated in Fig. 7, ϕ 1 to 5. In perfectly fresh specimens they are visible under a lens, and the largest of them, ϕ 1, with the unaided eye, as pinkish spots. They occur also in *L. galei* and *L. mustelicola*, but so far I have not observed them in *L. globosa* which dwells in darkness. It is possible that they act as photo-receptors since they are supplied by the antennal nerve. As far as I know these organs (?) have not been recorded hitherto in any species. In specimens of *L. galei* and *L. scyllicola* stained by me with Romanowski for 24 hours, and afterwards washed in two changes of 90 per cent. alcohol for a week, it was found that the muscles and tissues were faintly stained with eosin, while nowhere did any traces of methylene-blue linger except in the five places mentioned. These places superficially appear to be chitinous, but it is noticeable that none of the rest of the chitin (represented by stippling in Fig. 7) is so stained, neither is methylene-blue a stain for chitin.

The blue staining parts appear to represent organs below the chitin, these organs having a selective affinity for methylene-blue.

The Mandibles. On further examination I find that the mandibles, as previously figured by me in Part I, Fig. 3 C, are inaccurately drawn. I was for some time perplexed since it appeared to me that two types of mandibles

existed in this species. I am now certain that the true type of mandible is that which is figured in Fig. 3 A of the present paper, which closely approximates to that of *L. galei* except in regard to the secondary teeth, and in this respect I am not positive that one is not lost in *L. galei*. There are however but three primary teeth instead of four. My error was due to the fact that the terminal tooth was lost, as is not infrequently the case, and apparently the next principal tooth also; the organ being slightly turned on its side the intermediate teeth were unrecognisable, and what I considered to be teeth increasing in size posteriorly are really the secondary teeth. The wearing

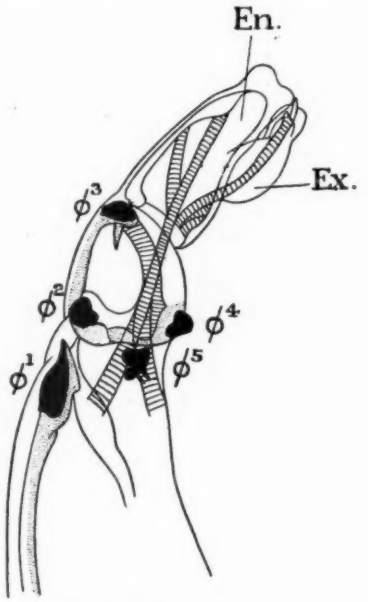
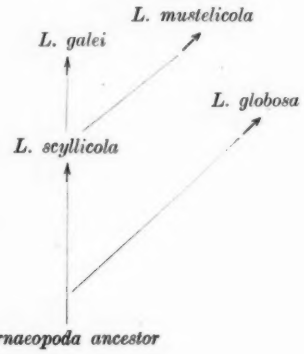


Fig. 7. *L. scyllicola*, a detailed enlargement of the antenna (Romanowski): *Ex.* exopodite; *En.* endopodite; ϕ1–5. (?) photoreceptors.

away of distal teeth is not to be wondered at if they have to pierce the skin of the dogfish where it is covered by dermal denticles.

Relationship. It appears to me that *L. scyllicola* and *L. galei* approximate to one another very closely, much more so than any other of the four species which I am at present considering. My opinion based upon the comparison of these species is that from the common *Lernaeopoda* stock, from which *Lernaeopodina* may have differentiated very early, *L. scyllicola* represents a central and most typical form from which *L. galei* and *L. mustelicola* subsequently descended, while I am inclined to think that *L. globosa* branched off from the stem prior to the evolution of *L. scyllicola*. The following diagram

represents my view of the mutual relationship existing between these four species:



Note on the Males.

Dr Charles Branch Wilson has kindly sent me a communication calling attention to the relative position of the second maxillae and maxillipedes in the males of the Lernaeopodidae. On consulting Fig. 38, Pl. XXXVI, of his paper on the development of *Achtheres ambloplitis* (*Proc. U. S. Nat. Mus.* XXXIX) it appears that it is the long *posterior* pair of appendages that correspond to the second maxillae in the females, and not the short anterior pair. In the subsequent development of the male these long maxillae remain posterior, while the short maxillipedes migrate forward between the bases of the maxillae and become anterior. Hence in the adult male the short, stocky anterior pair of mouth parts represent the migrated *maxillipedes*, and the longer and slenderer posterior pair represent the second maxillae which have remained where they were first formed. This, he shows us, is most clearly observed in the larval history, and if true of *Achtheres* it follows from analogy that it is probably true of the other genera including *Clavella*.

(My best thanks are due to Miss E. C. Humphreys for her kind assistance with the figures.)

Erratum.

Parasitology, XI, 120, five lines from the bottom of the page:
For "first maxillae" read "second maxillae."

A PRACTICAL HOT AIR DISINFESTOR.

By Major HAROLD ORR, O.B.E., M.B. (Toronto), C.A.M.C.

(With 5 Text-figures.)

The Hot Air Disinfestor herein described is the outcome of experiments undertaken in 1915, at the instigation of Colonel G. S. Rennie, C.M.G., then A.D.M.S., Canadians, Shorncliffe, in an effort to devise a satisfactory solution of the louse problem.

During that period G. H. F. Nuttall, Quick Professor of Biology, Cambridge University, was engaged in a research on the life history of *Pediculus humanus*, and he very kindly communicated to me from time to time the results of his investigations. Early in 1915 he found that the louse and the nit were killed in 10 minutes in a dry atmosphere at 50° C. and 55° C. respectively. It seemed clear in view of this that dry heat properly applied would have many advantages over steam or sulphur di-oxide, the means then employed, and must eventually supersede them for practical disinfesting purposes on a large scale in armies.

These advantages are obvious:

1. Rapidity of action. It is at least twice as rapid as steam and six times as rapid as sulphur di-oxide.
2. Simplicity in operation.
3. No article of clothing (including leather) is in any way damaged.
4. Clothing is not shrunken, creased or disfigured in any way.
5. Clothes are delivered warm and dry.
6. The fuel consumption is much lower than that of any other method of disinfestation.

Since 1915, I have introduced and employed several types of disinfestors. That described in this paper is the one now used throughout the B.E.F.

This disinfestor may be constructed in a few days' time from material readily available in R.E. dumps in the forward areas. Five men, one of whom is a carpenter, are required.

A sloping walled pit 5 feet deep (Fig. 1), measuring 7 ft. × 14 ft. at the top and 5 ft. × 10 ft. at the bottom is dug and the sides supported by trench revetting wire held in place by the usual steel pickets. Entrance to the pit is by a stairway at one side, and a tight-fitting door lined with corrugated

iron. Two 4″ pipes enter the chamber on the floor at each side of the door, to supply air to the braziers (Figs. 2, 3).

The chamber which measures 8 ft. × 15 ft. × 6 ft. inside, is constructed over the pit. The side walls and back of the chamber are 5″ thick. They consist of two layers of corrugated iron 5″ apart, the intervening space being

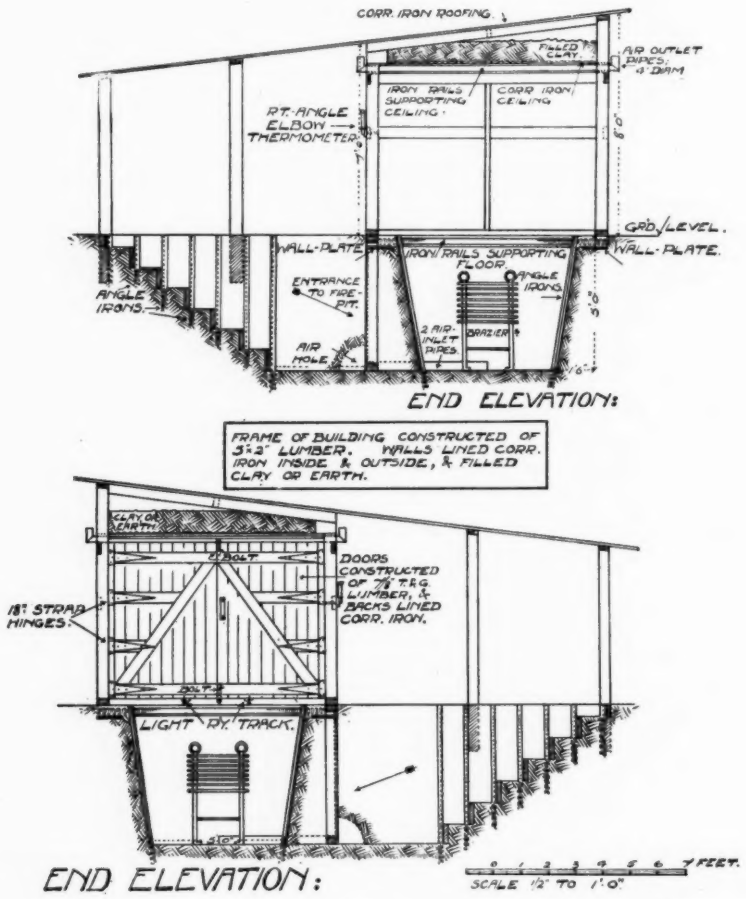


Fig. 1

solidly packed with earth or clay dug from the pit. The corrugated iron ceiling, which is supported by stout iron rails, is covered with one foot of earth, and a sloping roof is erected above this.

The corrugated iron floor (Fig. 2) is also supported by stout iron rails. 128 openings, each measuring 6″ × 3″ are made in the floor. A space 4 ft.

square, over the point where each of the two braziers stand, is left without openings.

Three 4″ outlet pipes extend through each of the side walls close to the ceiling,—one at each end and one midway between these,—each connected with an elbow outside.

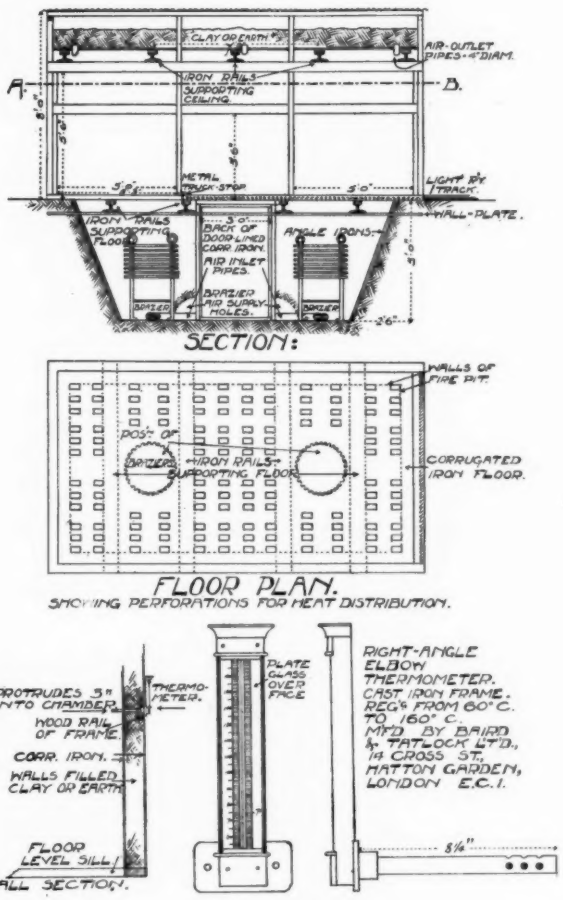


Fig. 2

The front of the chamber consists of two pair of tight-fitting doors. The inner pair made of tongued and grooved lumber, and lined with corrugated iron. The outer pair made of tongued and grooved lumber are separated from the inner pair by 3″, and overlap them at the sides and top. Their purpose is to render the chamber more air-tight. (The outer pair are not

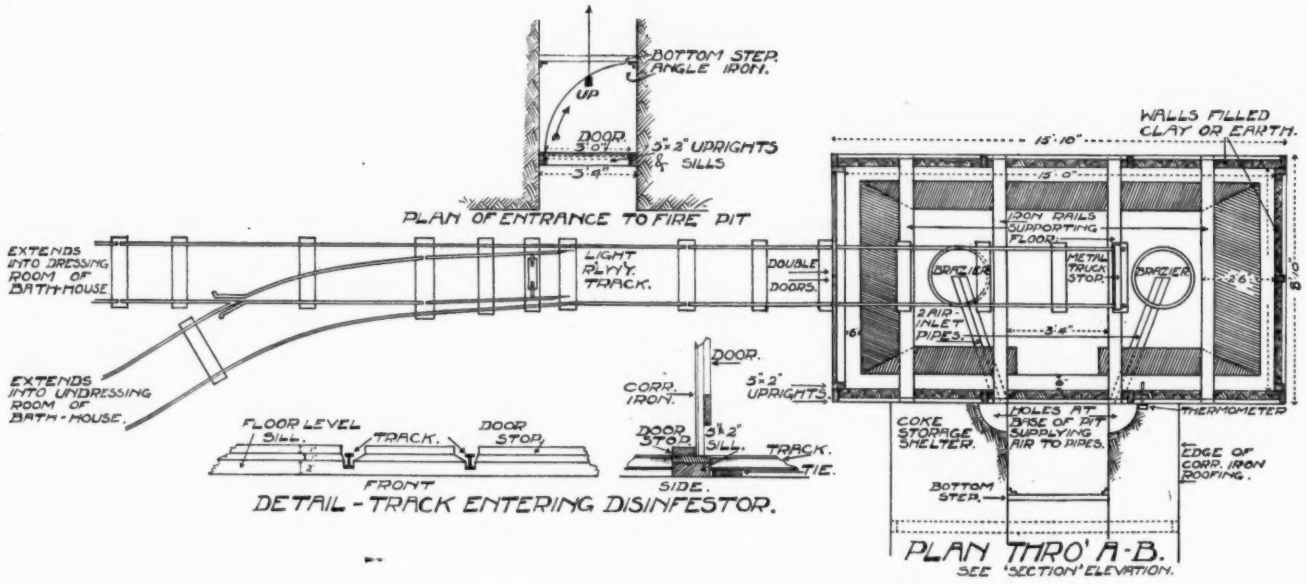

BOTTOM STEP ANGLE IRON.
UP
DOOR 3'0"
3"x2" UPRIGHTS & SILLS
3'4"
PLAN OF ENTRANCE TO FIRE PIT
EXTENDS INTO DRESSING ROOM OF BATH-HOUSE
LIGHT RLY'Y. TRACK.
DOUBLE DOORS.
EXTENDS INTO UNDRESSING ROOM OF BATH-HOUSE.
FLOOR LEVEL SILL.
TRACK.
DOOR STOP.
FRONT
DOOR.
CORR. IRON.
3"x2" UPRIGHTS
DOOR STOP
3"x2" SILL.
TRACK.
TIE.
SIDE.
DETAIL - TRACK ENTERING DISINFESTOR.
WALLS FILLED CLAY OR EARTH.
15'10"
15'0"
IRON RAILS SUPPORTING FLOOR.
BRAZIER
METAL TRUCK STOP.
BRAZIER
2 AIR-INLET PIPES.
3'6"
6'
9'8"
COKE STORAGE SHELTER.
HOLES AT BASE OF PIT SUPPLYING AIR TO PIPES.
THERMOMETER
EDGE OF CORR. IRON ROOFING.
BOTTOM STEP.
PLAN THRO' A-B.
SEE 'SECTION' ELEVATION.

Fig. 3

shown in the plan, but experience with the disinfestor in windy weather has proved them to be necessary.)

A special right-angle elbow thermometer (Fig. 2), scale 60° C. to 160° C. should be procured and built into the side wall of the chamber as shown in the plan (Fig. 1; see specification).

Light railway tracks (Figs. 2, 3, 5) are laid into the chamber, 11 ft. of track are in the chamber and at least 9 ft. outside, connected with a switch or a turntable. From the switch two tracks extend—one into the undressing-room and the other into the dressing-room of the bath house.

Two trucks (Fig. 4) are required, on each of which a rack is built to carry the clothing, etc. for disinfestation. The rack is one foot shorter and narrower than the chamber, and is so built on the truck as to be 6″ from the ceiling. The nails or pegs on the rack are 11″ apart.

The truck is loaded in the undressing room—the clothing being turned inside out and hung loosely on the pegs—one garment to a peg. As an alternative, hangers may be used in place of the fixed cross-bars carrying the pegs. Each hanger having hooks for all the clothing and blankets of one man. The clothing, etc. is hung on the hanger by the man as he undresses and the hanger handed to the attendant, who suspends it from one of the two longitudinal bars of the truck. The loaded truck is then wheeled into the disinfestor, and the other truck (empty) is wheeled out of the dressing room and switched into the undressing room, where it is in turn loaded and made ready to take its place in the disinfestor. When the disinfestation is complete (twenty minutes at 75° C. or higher) the truck is wheeled into the dressing room, unloaded, and switched back again into the undressing room, the freshly loaded truck having, in the meantime, been wheeled into the disinfestor.

These two rooms should be separated by a partition which extends to within 18″ inches of the floor. The boots and small box respirators, which need not be disinfested, are placed under the partition ready to be received by the men in the dressing room after the bath.

If the location of the dressing and undressing rooms does not permit of this, the boots and small box respirators should be carried into the bathroom by the men, and placed on shelves during the bath. This method has been adopted in one Division and works out very well.

Owing to the paucity of bath-house personnel, each man is as a rule, made responsible for the safety of his personal belongings. Supervision is necessary, however, to ensure that all articles of clothing and the blankets of each man, are disinfested. Two men are required as operators.

The braziers (Fig. 4) are 24″ in diameter, and will hold 100 lbs. of coke. At 7 A.M. all disinfestor doors should be open, fires started with a little wood, and each brazier three-quarters filled with coke. At 8 A.M. all the disinfestor doors should be closed. At 8.30 A.M. the disinfestor will be ready for use. The fires require no further attention during the day, beyond the addition of a little fresh coke at noon.

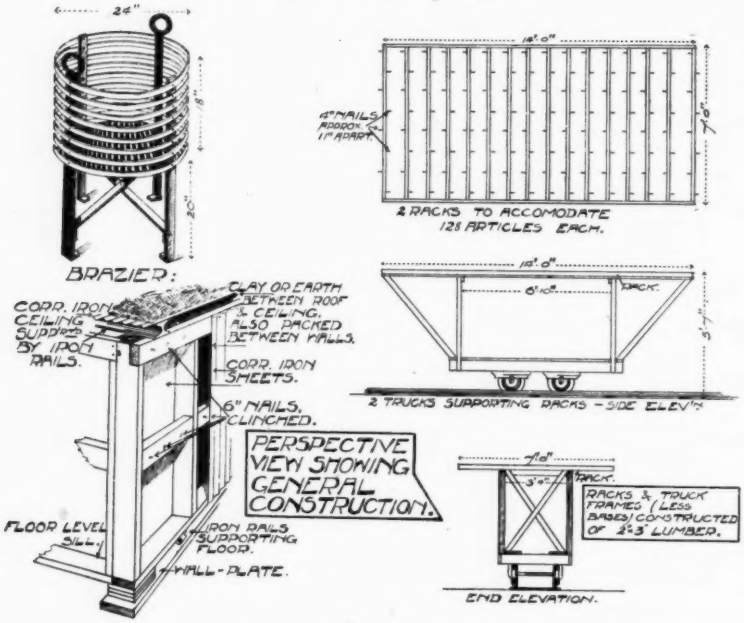
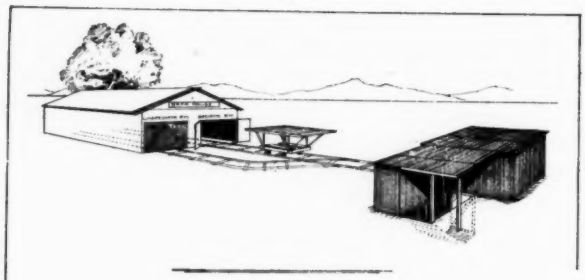
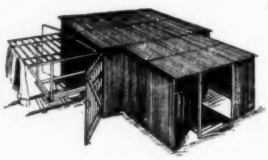

24"
BRAZIER:
CORR. IRON CEILING SUPPRT BY IRON RAILS.
CLAY OR EARTH BETWEEN ROOF & CEILING. ALSO PACKED BETWEEN WALLS.
CORR. IRON SHEETS.
6" NAILS, CLINCHED.
PERSPECTIVE VIEW SHOWING GENERAL CONSTRUCTION.
FLOOR LEVEL
IRON RAILS SUPPORTING FLOOR.
WALL-PLATE.
4" NAILS ABOUT 1" APART
2 RACKS TO ACCOMODATE 128 ARTICLES EACH.
RACK.
2 TRUCKS SUPPORTING RACKS - SIDE ELEV'N
RACKS & TRUCK FRAMES (LESS BASES) CONSTRUCTED OF 2"x3" LUMBER.
END ELEVATION.

Fig. 4



PERSPECTIVE DRAWINGS ILLUSTRATING DISINFESTOR IN CONJUNCTION WITH BATH-HOUSE:



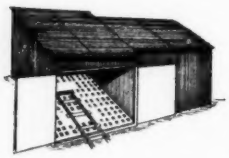


Fig. 5

It is important that the disinfestor be built according to plan, attention being paid to:

(*a*) Selection of site in relation to bath house;
(*b*) The packing of the walls with clay;
(*c*) The arrangements of the openings in floor;
(*d*) The position of the switch or turntable. Its distance from the door of the chamber must be at least half the length of the rack plus half the wheel-base of the truck;
(*e*) The location of the air inlet and air outlet pipes;
(*f*) To prevent warping, the framework of the truck should be made of heavy wood. Iron should be used if possible;
(*g*) The door of the entrance to the pit, and the two pairs of doors to the chamber, must be tight fitting.

The difficulties met with in employing hot air as a means of disinfestation are due to the fact that the specific heat of air is very low, and on account of that a constantly moving supply of freshly heated air is necessary in order to raise solid articles quickly to a temperature that is lethal to vermin.

In this disinfestor, the hot air and gases from the coke braziers in the pit are distributed by the perforated iron floor, and then sweep upwards through the disinfesting chamber, and ultimately escape through the series of vent pipes distributed along the top of the walls. Thus, there is a regular and rapid change of hot air at the surface of clothing suspended in the chamber.

The total sectional area of the vent pipes is greater than that of the cold air inlet pipes in the ratio of three to two. This ratio is somewhat greater than is necessary to allow for the increase in volume of the air on being heated and on being enriched with gases from the burning coke. No resistance, then, is offered to the escape of the slightly expanded air.

I have made daily temperature observations during the working of a large number of these disinfestors. In some of them the observations covered a period of two months. The measurements were taken with ordinary chemical thermometers placed in various parts of the chamber, and with naphthalene tubes melting at known temperatures. In the majority of tests, lice and nits were placed in the clothing with the thermometers.

The results may be summarized as follows:

1. In fair weather, when the clothing is dry, a temperature (55° C.) sufficient to kill lice and nits in ten minutes is invariably attained beneath the folds of the clothing in from one to five minutes.
2. In stormy weather when the clothing is wet and cold, this lethal temperature is invariably attained in from five to fifteen minutes.
3. The temperature beneath the folds of the clothing lags from ten to fifteen degrees centigrade below that of the surrounding air, as registered by the right angle elbow thermometer built in the wall of the disinfestor.

4. It has not been demonstrated that any article of clothing is in any way damaged by this process.

For practical purposes, the material for disinfestation should be exposed to a temperature as recorded by the wall thermometer, of 75° C., or higher for twenty minutes. Since the louse and the nit are killed at 50° C. and 55° C. respectively (Nuttall), this leaves a considerable margin of safety.

Through the kindness of the Director General Medical Services B.E.F., I am permitted to publish the results of an independent investigation undertaken by Captain T. J. Murray, M.Sc., Ph.D., R.A.M.C., T.F., working under the direction of Colonel W. W. O. Beveridge, C.B., D.S.O., A.D.M.S. Sanitation, B.E.F., with a view to observing the working of this disinfestor and more especially in order to measure the temperature reached in the clothing during the process of disinfestation.

The apparatus employed for the measurement of the temperatures was brought to France especially for this purpose by Colonel Beveridge, and was formerly used by him in the measurement of temperatures reached in the interior of foods during the process of cooking. It consists of an electro thermo-couple, with a milli-voltmeter in circuit. The electro thermo-couple is made of two long pieces of wire of different metals soldered together at their ends, and insulated throughout their length. One wire consists of copper and the other of an alloy known as constantan. In such a circuit, if one junction is at a higher temperature than the other, a current of electricity is generated in the wire. The greater the difference in temperature at the junctions, the stronger is the current in the wire. The milli-voltmeter indicates the strength of the electric current set up in the wire circuit.

If one junction is kept at a constant low temperature, by placing it in melting ice at 0° C. the current strength varies with the temperature of the hot junction.

In these experiments, the milli-voltmeter and the cold junction were placed outside the chamber, the insulated wires were passed through an opening into the disinfestor, and there was sufficient length of wire to allow of the other junction being placed at any point of the clothing, in any region of the chamber.

By simply noting the readings on the milli-voltmeter, the temperature at the point of the clothing occupied by the hot junction can be registered. The process is continuous, and all variations in temperature can be observed.

Captain Murray reports:

"Eleven completed chambers were examined and of these two had faults of construction which would have rendered them inefficient. In one of the faulty disinfestors, the braziers were made half-size, and would thus be incapable of maintaining the requisite supply of hot air. In the other, the walls were badly packed and the truck-rails entered the chamber at an angle, so that the clothing rested against one wall, and left a free space of

two feet at the other side, rendering an even distribution of heat impossible. It was evident that these errors were due to carelessness in construction, and not to any faults in the drawings. Although several of the other disinfestors examined had been erected by unskilled labour, they were built according to specification, and were working efficiently.

Temperature measurements were made on thirty different occasions, these tests being distributed over six disinfestors. In 28 cases out of thirty, the temperature reached in the garments was sufficient to destroy any lice and their eggs. The failure of the other two charges was to be expected before the beginning of the experiments, as the working instructions were not being observed. In both cases there was only a thin layer of coke at the bottom of the braziers, and a sufficient supply of hot air could not be maintained. One of these tests was carried out in the badly constructed disinfestor referred to above, in which the rails entered obliquely, and in which the heat distribution was unsatisfactory. Even in these adverse circumstances, lice were killed in the clothing, but doubt remained as to the destruction of the nits. In chambers constructed according to specification, and worked in accordance with instructions, the results were invariably good.

With the thermo-couple employed, the temperature at any point in the clothing, and in any region of the chambers could be observed continuously from the beginning to the end of the process of disinfestation.

The following are details of measurements carried out at four of the disinfestors:

Test A. Surprise visit to disinfestor at Gouy Servins at 12.30 P.M. on 13.vii.18.

The attendants had stopped work for dinner.

The braziers had not been touched since 8 A.M., and were half-full of coke.

A truck was loaded with shirts, one shirt on each peg.

The point of the thermo-couple was placed in the folds of a shirt.

In	1 minute	the temperature	had reached	54° C.
In	5 minutes	,,	,,	67
In	10 ,,	,,	,,	75
In	15 ,,	,,	,,	81
In	20 ,,	,,	,,	85

All lice were shrivelled, also nits.

Test B. Surprise visit to bath house at Neuville St Vaast, at 11.25 A.M. on 14.vii.18.

Bathing was in operation, men were arriving in parties of 50 every half-hour. All men were bathed, issued with clean clothing, and were compelled to have their service dress passed through the disinfestor. The wire of the

thermo-couple was passed up the leg of a pair of riding breeches, and the junction-point was fastened at the crutch of the breeches.

In	2	minutes the temperature had reached	54° C.
In	5	,, ,, ,,	64
In	10	,, ,, ,,	72
In	15	,, ,, ,,	78
In	20	,, ,, ,,	83

All lice were killed and eggs shrivelled. No damage was done to the leather of riding breeches or to the braces. The bathing operation was not delayed by the disinfestation process.

Test C. Disinfestor at Corps Skin Hospital, Estree Cauchie.

2560 blankets were disinfested in a day of 7½ working hours. 128 blankets formed a load—20 loads were disinfested, and each load was controlled by temperature measurements. The braziers were lit at 7.30 A.M., operation commenced at 9.13 A.M. The braziers were re-charged during the lunch interval. In all 195 lbs. of coke were used during the day.

The point of the thermo-couple was placed in the folds of the blankets which were suspended from hooks in the truck.

The following results of measurements of one of the charges can be taken as typical of the series:

In	2	minutes the temperature was	57° C.
In	10	,, ,,	69
In	15	,, ,,	79
In	20	,, ,,	83

Test D. Disinfestor at Corps Skin Hospital, Estree Cauchie.

Load of "wet" clothing. The charge consisted of 20 blankets and 33 articles of hospital clothing, which were thoroughly wet, through standing in the rain. The blankets were hung from their centres and the thermo-couple was placed *inside* the cone formed by one of the blankets. The point of the couple was about 18″ from the apex of the cone. The temperature immediately after closing the door was 25° C.

In	5	minutes the temperature was	44·5° C.
In	11	,, ,,	56·0
In	15	,, ,,	60·0
In	20	,, ,,	64·5
In	25	,, ,,	71·0
In	30	,, ,,	77·0

This was a very severe test and shows that the disinfestor is capable of dealing with wet clothing, provided the time be slightly extended. The blankets came out dry.

Test E. "Small size" Canadian Disinfestor at Dressing Station of 74th Field Ambulance, Grand Servins.

The charge consisted of blankets and shirts.

The thermo-couple was placed in the folds of a blanket as in Test C.

In	4	minutes	the temperature had reached	55·5° C.
In	10	,,	,,	61·0
In	15	,,	,,	66·0
In	20	,,	,,	71·0
In	25	,,	,,	73·0
In	30	,,	,,	78·0

All lice were killed and eggs shrivelled.

The foregoing are typical results of measurements taken under various conditions. They show that during the normal working of "the Canadian Disinfestor," the temperature reached in the clothing is higher than that necessary to destroy lice and their eggs (nits and lice are killed at 55° C. in 10 minutes) but not sufficiently high to damage clothing material.

Measurements were taken at various points in the chambers, but no cold region could be detected. When clothing is damp the water quickly evaporates and the water vapours can be recognised leaving the chamber with the hot gases, at the vent holes.

The interval between removing one charge and replacing it by another need not be longer than one minute, the unloading and loading of one truck is taking place while the second truck is in the disinfestor.

Braziers properly charged with coke in the early morning require no further attention during the day, unless work is being continued till late in the afternoon, when the addition of more coke at noon is necessary.

My thanks are due especially to Professor G. H. F. Nuttall for having early placed much scientific information at my disposal. The pioneer of Disinfestors (now of course obsolete) built in 1915, was based on the facts, regarding the lethal temperatures of the louse and nit, supplied to me by him.

I wish also to thank Private G. A. H. Baxter, C.A.M.C., for executing the drawings; Privates W. H. Marshall, F. Sefton and R. A. Coward, C.A.M.C., have kindly prepared a working model, which may be seen in the Imperial War Museum.

MATERIAL REQUIRED.

For building disinfestor 8 ft. × 15 ft. Capacity 384 blankets per hour. Fuel consumption—200 lbs. coke per day.

48 sheets	7 ft. corrugated iron
58 sheets	6 ft. corrugated iron
9 lengths	9 ft. each, 3 × 5 gauge rail
3 rolls or 75 yds.	18 in. trench revetting wire

40 lengths	6 ft. angle irons
250 feet	Plain wire
7 lengths	16 ft. 2″ × 5″ scantling
250 feet	2″ × 5″ scantling
500 feet	$\frac{7}{8}$″ tongue and groove
550 feet	2″ × 3″ scantling
30	3 ft. wood stakes
30 lb.	4″ nails
20 lb.	6″ nails
30 lb.	$2\frac{1}{2}$″ nails
5 lb.	$1\frac{1}{2}$″ nails
5 pairs	18″ T-hinges, $1\frac{1}{2}$″ screws
2 pairs	3′ 6″ hooks and band hinges
3 pairs	Door bolts
10 lengths	4″ stove pipe
6	4″ elbows
2 braziers	Each of at least 24″ diameter
1	16 ft. length light rail, straight
1	16 ft. length light rail, switch (right or left)
3	16 ft. lengths curve rail
2	Push trucks

1 cast iron frame, right-angle elbow thermometer, range 60° C. to 160° C.; length of stem $8\frac{1}{4}$″ from flange. (Baird & Tatlock, Ltd., 14–15, Cross Street, London, E.C.)

HERMAPHRODITISM AND OTHER ABNORMALITIES IN *PEDICULUS HUMANUS*.

By D. KEILIN, Sc.D., and G. H. F. NUTTALL, F.R.S.

(*From the Quick Laboratory, University of Cambridge.*)

(With Plates XII–XVII and 28 Text-figures.)

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INTRODUCTION.

This paper is based on the study of a large material derived from various sources and containing a great number of abnormal specimens of *Pediculus humanus*, namely 155 hermaphrodites, besides abnormalities other than sexual which occur very rarely among insects.

After having completed a systematic study of (*a*) specimens raised by us in the Quick Laboratory and of (*b*) specimens of "wild" lice that had reached

us from different parts of the world, we came upon (*c*) further specimens in a large material received from Mr A. Bacot, Entomologist to the Lister Institute.

In describing material (*a*) and (*b*) above specified, we were guided by morphological considerations in respect to the sequence in which the various abnormalities are described, whilst the order in which (*c*) Bacot's material is treated corresponds to that of the various families and generations in which the specimens were contained, all being derived from crosses between *capitis* and *corporis*, some raised up to the third generation in the laboratory.

The foregoing material permits us to describe a complete series of hermaphrodites, to explain certain anomalous structures in them, and to advance a reasonable hypothesis as to the origin of hermaphroditism in *Pediculus humanus*. Our studies have opened up a fruitful field of investigation bearing on the sex problem.

Acknowledgments.

We have pleasure in acknowledging the invaluable assistance we have received from Mr A. Bacot, who placed his material at our disposal for purposes of study, and on several occasions sent us living specimens of *P. humanus*, both *capitis* and *corporis*, wherewith to conduct experiments. We are also indebted to the Hon. H. Onslow for kindly directing our attention to some of the recent literature relating to gynandromorphism.

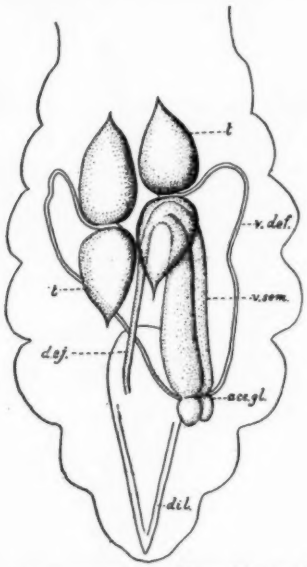
Sexual dimorphism in *Pediculus humanus*.

Before proceeding to the consideration of the 155 hermaphrodites we have studied, it is necessary, in the first place, to dwell briefly upon the characters that differentiate the sexes in normal lice:

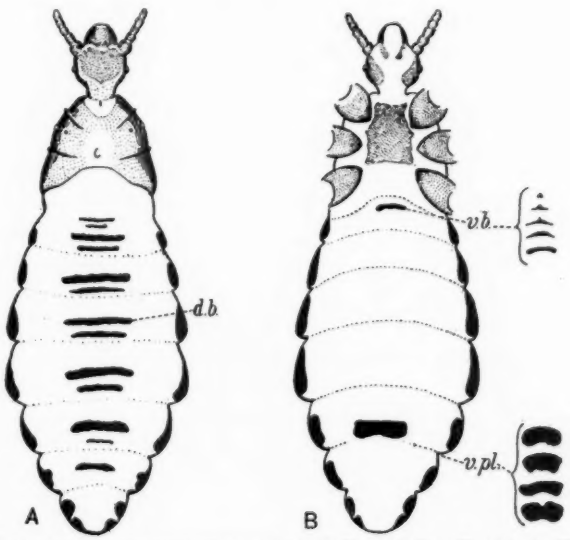
Primary and secondary sexual organs.

MALE (Text-fig. 1): *Internal sexual organs*. The male possesses two pairs of testes, each testis being piriform in shape, the pair approximating to each other basally where they open into a common vas deferens (*v.def.*). The vasa deferentia, leading from the paired testes on each side, terminate in corresponding branches of the forked vesicula seminalis (*v.sem.*), the vesicula in turn leading to the ductus ejaculatorius (*d.ej.*). Where the latter joins the vesicula, this is bent abruptly backward, so that the duct and vesicula lie parallel to each other in the median line.

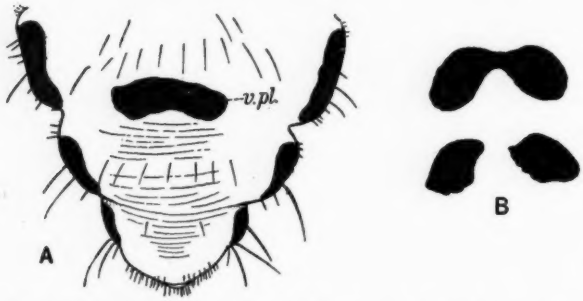
External genitalia. When devaginated, the copulatory apparatus consists of a chitinous, dentate vesicula, a penis protruding dorsally between the branches of the dilator which hinges proximally upon a basal plate. The protruding penis is borne laterally upon the vesica penis. When retracted, these parts can be more or less distinctly seen by transparency. The pointed



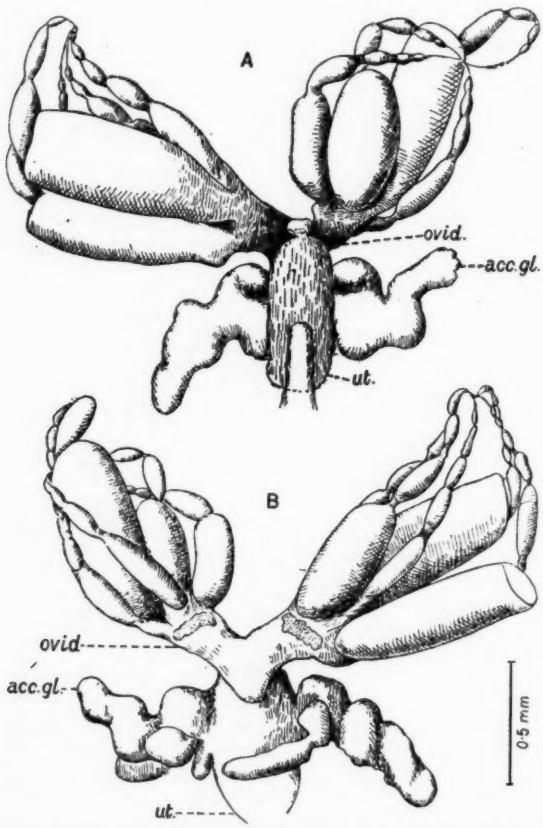
Text-fig. 1. *Pediculus humanus* race *corporis* ♂. Normal internal sexual organs, showing their position in the abdomen as seen by transparency from the dorsal side. The basal plate, dilator and vasa deferentia are schematized. *acc.gl.* = accessory gland, *d.ej.* = ductus ejaculatorius, *dil.* = dilator, *t.* = testis, *v.def.* = vasa deferentia, *v.sem.* = vesicula seminalis. (K. & N. del.)



Text-fig. 2. *Pediculus humanus* race *capitis* ♂ (Lot 237, Nairobi, Brit. E. Africa). Normal, deeply pigmented specimen (A) in dorsal and (B) in ventral aspect. *d.b.* = dorsal bands, *v.b.* = ventral band, *v.pl.* = ventral plate; the last two structures vary in form as figured. (N. del.



Text-fig. 3. *Pediculus humanus* race *capitis* ♂ (Lot 237, *v. supra*). Normal specimen. (A) Posterior part of abdomen in ventral aspect showing ventral plate (*v.pl.*); (B) the ventral plate is occasionally bilobed or bipartite in normal specimens. (*N.* del.)



Text-fig. 4. *Pediculus humanus* race *corporis* ♀. Normal internal sexual organs removed by dissection, and seen (A) in ventral and (B) in dorsal aspect. *acc.gl.* = accessory gland, *ovid.* = oviduct, *ut.* = uterus (N. & W. del.)

end of the dilator frequently protrudes from the body. The abdomen bears a ventral plate and is rounded posteriorly. See Text-figs. 2, 3[1].

FEMALE (Text-fig. 4). The female possesses two ovaries, each consisting of five ovarial tubes which terminate in oviducts (*ovid.*) that unite and enter the uterus (*ut.*) dorsally. The uterus communicates ventrally with the vagina and laterally with the paired accessory glands (*acc.gl.*). The vaginal orifice lies ventrally in the form of a transverse slit situated beneath two gonopods which curve towards each other in the median line. Anterior to the gonopods lies the ventral plate. The abdomen ends in two posterior lobes. See Text-fig. 5[1].

Text-fig. 5. *Pediculus humanus* race *capitis* ♀ (Lot 237, *v. supra*). Normal specimen. (A) Posterior part of abdomen in ventral aspect: gonopods (*gon.*), ventral plate (*v.pl.*), posterior lobes (*p.l.*). (B) Normal variation in form of ventral plate. (N. del.)

Secondary somatic characters.

Size. The ♂ is usually smaller than the ♀, but the character is inconstant.

Leg I. In the ♂, the first leg differs from the others in being more powerful and possessing a large thumb whereby the female's third leg can be firmly grasped during copulation. Leg I in the female does not differ from the others.

Leg III. This leg is characterized, in the ♀ only, by a spur situate ventrally near the base of the femur[2].

Dorsal bands (Text-fig. 3). Normally, these are only present in the ♂. They consist of a series of paired transverse bands occurring dorsally upon the abdominal segments and are especially evident in well-pigmented specimens.

Abdominal muscles. In the ♂, the dorsal longitudinal muscles form an uninterrupted series extending from the thorax to the last segment, and the ventral longitudinal muscles occur in four successive rows starting at the

[1] For descriptions and illustrations of the normal ♂ and ♀ genitalia and intersegmental abdominal muscles, see Nuttall, *Parasitology*, IX. 293–296, where their functions are explained.

[2] Text-fig. 23 will serve to illustrate the characters of ♂ leg I and ♀ leg III respectively.

thorax. In the ♀, the corresponding muscles occur dorsally only in the last three segments; ventrally in two of the middle segments and anteriorly, adjoining the thorax, the series in other words being interrupted (in *corporis*) by the absence of such muscles in one segment.

I.

HERMAPHRODITISM IN *PEDICULUS HUMANUS.*

Previous observations. The only reference in the literature to the occurrence of hermaphroditism in lice is that contained in a brief passage of a preliminary note of Sikora's (v. 1917, p. 173). This author states[1] that she observed hermaphrodites among "wild" lice and others raised in captivity. The abnormal individuals varied in structure. On the one hand what appeared to be an otherwise normal male would possess an abnormal "gonopodial spot and rudimentary vulval folds," on the other hand a female would exhibit abnormally pigmented tergites which afforded the only external sign of the bi-sexual structure of the internal genital organs, this condition being accompanied by abnormalities affecting (*a*) almost invariably the structure of the thumb of leg-pair I and (*b*) occasionally the abdominal musculature. Sikora, having collected 70 abnormal specimens of the kind, proposed to make them the subject of special study. We are not aware, however, of her having published any further particulars on the subject.

Method of examination.

As all the material here described had been preserved in alcohol, we employed the simple method of examining the specimens when impregnated with cedarwood oil. This was of advantage since it rendered it possible to study the internal organs *in situ* without their being displaced, and facilitated the discovery of the invaginated structures that would otherwise have been invisible from the outside.

Whilst a number of the foreign specimens grouped under (*b*) in the subjoined list had the internal organs macerated, a few of them were sufficiently well preserved to permit of their internal structures being studied. In a few cases attempts were made at dissection but only with moderate success.

[1] Sikora writes: "Ich möchte auch noch erwähnen, dass ich sowohl unter den wilden als auch unter den in Gefangenschaft aufgezogenen Läusen Hermaphroditen fand, vom anscheinend normalen ♂ mit einem Gonopodenfleck und rudimentären Vulvaklappen bis zum ♀, an dem nur Pigmentierung der Tergite äusserlich den zwitterigen Bau der Keimdrüsen verrät, der fast immer von Abnormitäten am Daumen des ersten Beinpaares und zuweilen auch der Abdominalmuskulatur begleitet ist. Ich werde das zahlreiche Hermaphroditenmaterial (etwa 70 Stück) systematisch bearbeiten."

By way of comment it may be noted that unpigmented "tergites" (our dorsal bands) are not present in females as Sikora would seem to imply. We are here dealing with a structural character in relation to which pigmentation has no significance since it may or may not be in abeyance whilst the structure persists.

We hope soon to be able to study fresh material and thus obtain a further insight into the internal anatomy of the hermaphrodites.

To obtain an accurate survey of the very varying structures observed in the individual hermaphrodites, we made systematic notes on each specimen and drawings of most of them. The drawings were all executed by ourselves with the aid of the camera lucida, and the accompanying illustrations represent a selection from the many we have made. Whereas the plates represent, as nearly as practicable, the natural appearance of the specimens, the text-figures are mostly somewhat schematized in so far as the deeply pigmented chitinous plates, pleurae, gonopods, etc. are represented in black.

Material.

The hermaphrodites and other abnormalities about to be described were derived from the following sources:

LOT

(*a*) Specimens raised in Cambridge.

265. *Corporis* of British origin, bred in the Quick Laboratory; having been raised on black cloth they were darkly pigmented. Six hermaphrodites (Nos. 4, 18, 21, 23, 24, 29).

(*b*) "Wild" lice collected abroad.

237. *Capitis* + *corporis*, from negro, Nairobi, British East Africa. The lot consisted of 94 ♂, 120 ♀, and 2 hermaphrodites (Nos. 12, 31).

277. *Corporis*, from Kikuyu negro, Nairobi, British East Africa. The lot consisted of 94 ♂, 151 ♀, and 2 hermaphrodites (Nos. 8, 13).

278. *Corporis*, from Kikuyu negro, Nairobi, British East Africa. The lot consisted of 141 ♂, 224 ♀, and 1 hermaphrodite (No. 11).

257. *Capitis*, from Masai negro, Tanga, German East Africa. The lot consisted of 71 ♂, 102 ♀, and 2 hermaphrodites (Nos. 20, 22).

273. *Corporis*, from asylum patients, Sydney, New South Wales. The lot consisted of 65 ♂, 134 ♀, and 19 hermaphrodites (Nos. 1, 2, 3, 5, 6, 7, 9, 10, 14, 15, 16, 17, 19, 25, 26, 27, 28, 30, 32).

The 32 hermaphrodites included in the foregoing list, (*a*) and (*b*), are described in the order of the numbers bracketed after the data regarding their source.

(*c*) Bacot's material.

This material was derived from various crosses between *capitis* and *corporis* raised by Bacot in London. As a full record thereof will be found on p. 315, 316, it will suffice here to state that the material was found by us to comprise 123 hermaphrodites.

Systematic Description of 32 Hermaphrodites: Material (a) and (b).

To facilitate the description of our 32 specimens, we have arranged them in groups as follows:

Group I. With posterior end of abdomen rounded as in the normal ♂, with ♂ and ♀ genitalia present and *having the general appearance of a male as indicated by the sign* ⚥.

(*a*) With ♂ and ♀ genitalia equally well developed except for the posterior abdominal lobes of ♀.

(*b*) With ♂ genitalia complete but with ♀ genitalia reduced and invaginated in the median line.

(*c*) With ♂ genitalia complete, the ♀ genitalia being represented by a unilateral gonopodial invagination.

(N.B. Specimens 95, 96, 118, 119, 149, hereinafter described, see pp. 301, 304, 307, represent an intermediate Group between Groups I and II.)

Group II. With posterior end of abdomen bilobed as in the ♀. With ♀ genitalia well developed, ♂ genitalia obsolete or much reduced and enclosed in the body. *Having the general appearance of a* ♀ *as indicated by the sign* ⚤.

Group I (18 ⚥ specimens).

(a) *With* ♂ *and* ♀ *genitalia equally well developed except for the posterior abdominal lobes of* ♀.

SPECIMEN 1, ⚥. Pl. XV, fig. 1; Pl. XVII, fig. 4.

Dorsal bands complete. Legs: pair I as in normal ♂, pair III as in normal ♀. ♂ genitalia abnormal, with basal plate and dilator (*dil.*) flattened, very wide, asymmetric, with point curved to the left side of the insect. ♀ genitalia consisting of almost normal gonopods (*gon.*), the right gonopod slightly smaller. ♂ ventral plate (*v.pl.* ♂) well chitinized and divided (bipartite) in two widely separated pieces of irregular form. ♀ ventral plate (*v.pl.* ♀) rhomboidal, totally separated from the foregoing. Two very small rudimentary ♀ posterior lobes (Pl. XVII, fig. 4) bearing sensory hairs and situate dorsally flanking the anus. Abdominal muscles: dorsally as in ♂, ventrally as in ♀; no other internal organs visible.

SPECIMEN 2, ⚥. Pl. XV, fig. 2; Pl. XVII, fig. 6.

Dorsal bands slightly fragmented. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia abnormal, with basal plate and dilator distorted, the dilator with penis protruding out of the body and curved to the left side. ♀ genitalia consisting of two normal gonopods. ♂ ventral plate bipartite, the left portion being fused to the ♀ ventral plate, the plates being of irregular form. Posterior end of abdomen obliquely truncated. Two rudimentary ♀ posterior lobes (*p.l.*, Pl. XVII, fig. 6) are visible dorsally. The specimen had the vagina and

part of the uterus prolapsed but these were removed prior to drawing the figure. Abdominal muscles: dorsally as in ♂, ventrally as in ♀; no other internal organs visible.

SPECIMEN 3, ♀. Pl. XV, fig. 3.

Dorsal bands and legs as in normal ♂. ♂ genitalia slightly deformed. ♀ genitalia with gonopods well developed, unequal, rotated somewhat out of their normal axes, the smaller gonopod with sensory hairs upon its dorsal surface instead of along its posterior border. ♂ ventral plate divided in two parts both clearly separated from the ♀ plate. Abdominal muscles: dorsally as in ♂, ventrally as in ♀ but abnormal in being confined to one middle segment less (as in Specimen 12, Text-fig. 8). *Internal organs:* two pairs of normal testes, vesicula seminalis deformed through being compressed by the vagina; a peculiar body near the anterior right-hand testis may represent a young egg.

SPECIMEN 4, ♀. Not illustrated.

Dorsal bands as in ♂. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia well developed, with dilator point slightly distorted. ♀ genitalia with gonopods well developed and rotated out of their axes as in Specimen 3. Dorsal and ventral abdominal muscles as in ♂.

SPECIMEN 5, ♀. Pl. XVI, fig. 1, and Text-fig. 6.

Dorsal bands complete but showing abnormal tendency to fuse. Legs: pair I as in ♂, pair III with slight ♀ character. ♂ genitalia abnormal, the basal plate narrow and the dilator twisted. ♀ genitalia with gonopods short, compressed, unequal, widely separated apically. Vagina prolapsed (*vag.p.*, Pl. XVI, fig. 1), raising the gonopods and ♀ ventral plate above the abdominal surface, this plate transversely elongate, with sharp lateral angles and deep emargination in the postero-median line. ♂ ventral plate divided, the portions widely separated. Dorsal and ventral abdominal muscles as in ♂.

Text-fig. 6. *Pediculus humanus* race *corporis* ♀. Specimen 5, the same as illustrated in Pl. XVI, fig. 1. Showing abnormal dorsal bands. (N. del.)

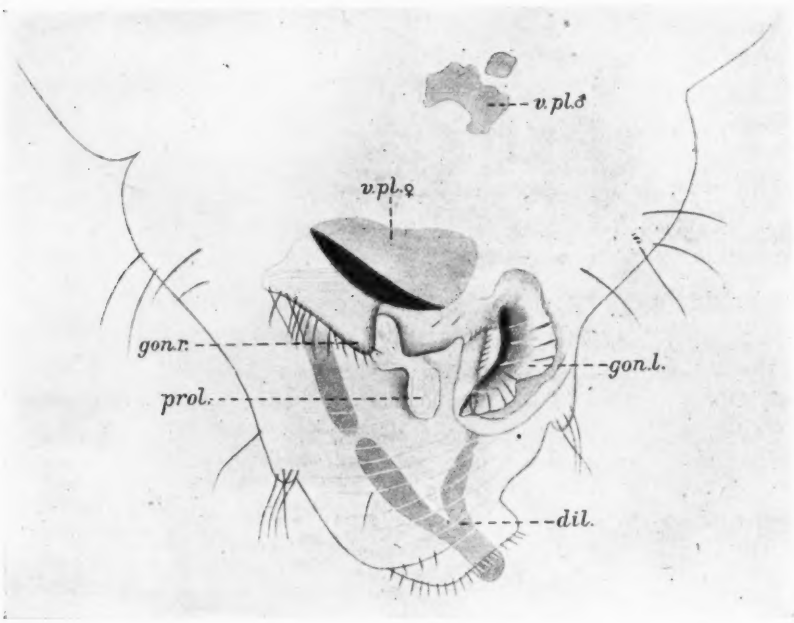
SPECIMEN 6, ♀. Not illustrated.

Similar to Specimen 5, but leg III is of ♀ type. The prolapse beneath the gonopods is long and tubular as in Specimen 2. Posterior end of abdomen ruptured and ♂ genitalia with vesica penis protruded (accidental injury). Dorsal muscles as in ♂, ventral muscles macerated but judging from remnants also of ♂ character.

SPECIMEN 7, ♀. Pl. XVI, fig. 3.

Dorsal bands as in ♂. Legs missing. ♂ genitalia reduced in size. ♂ ventral plate divided in two parts of unequal size. ♀ genitalia showing a very remarkable abnormality, the different parts observable being difficult to homologize

with normal structures. These parts are borne on a pedicle protruding from the abdomen, the pedicle being invisible in the illustration. The ♀ ventral plate forms an oval ring (*v.pl.*) with its left side flat, broadening and forming a cordiform plate. The centre of the ring is occupied by two conical prominences (*x*) each bearing a row of sensory hairs. The cordiform plate covers an irregularly shaped fleshy body, similar to a prolapsed vagina (*vag.p.*), but bearing at its external angles two small prominences with sensory hairs (*y*). The two conical prominences (*x*) appear to represent the terminal parts of the gonopods, and the two small prominences (*y*) their



Text-fig. 7. *Pediculus humanus* race *corporis* ♀. Specimen 8. Posterior end of abdomen, in ventral aspect. (K. del.)

basal portion. These two parts were probably separated and displaced by the malformation of the vagina. (Compare Text-figs. 14 C and 16 A in relation to the foregoing.) Dorsal and ventral muscles as in ♂.

SPECIMEN 8, ♀. Text-fig. 7.

Dorsal bands as in ♂, slightly chitinized. Legs I and III as in ♂. ♂ genitalia abnormal, with dilator (*dil.*) curved to the left. ♂ ventral plate (*v.pl.* ♂) reduced to small irregular fragments on the left side. ♀ ventral plate irregular, slightly chitinized, except at its left posterior border which appears folded

and more chitinized. ♀ genitalia with gonopods of very unequal structure and size; the right gonopod is small, but of normal structure; the left gonopod (*gon.l.*) is larger and deformed as follows: the major portion forms a gutter-like depression along whose borders are ranged sensory hairs with their apices directed into the gutter; alongside the gutter, but nearer the median line, occurs a pointed protuberance bearing sensory hairs, the base of the protuberance overlapping the posterior portion of the gutter. Between the gonopods there was a vaginal prolapse (*prol.*), which was cut away before the specimen was drawn. Dorsal and ventral abdominal muscles as in ♂. *Internal organs:* one testis and ova in various stages of development were observed. The posterior end of abdomen asymmetric, obliquely truncated; two processes bearing sensory hairs occur laterally and posterior to the gonopods.

(b) *With ♂ genitalia complete but with ♀ genitalia reduced and invaginated in the median line.*

SPECIMEN 9, ♀. Pl. XVII, fig. 1.

Dorsal bands as in normal ♂. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia asymmetric, especially in the anterior part of basal plate. ♂ ventral plate divided in two parts of irregular form; between these parts there is a deep invagination (*invag.gen.*) of dark chitin forming within the body of the insect a very irregular mass with two lateral pockets bearing sensory hairs internally; these pockets may be homologized with invaginated gonopods, whilst the main mass of chitin corresponds to the ♀ ventral plate. Dorsal and ventral abdominal muscles as in ♂.

SPECIMEN 10, ♀. Not illustrated.

Dorsal bands as in ♂. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia asymmetric, reduced, slightly oblique. ♂ ventral plate consists of two widely separated portions, separated by a chitinous invagination of very irregular shape, thickness, and colour; this invagination (as in Specimen 9) corresponds to different parts of the ♀ genitalia. Dorsal and ventral abdominal muscles as in ♂.

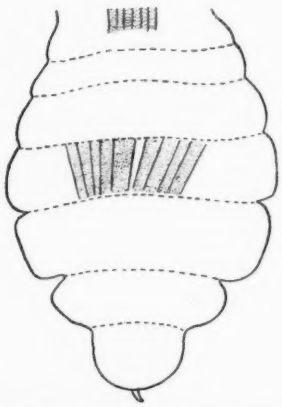
SPECIMEN 11, ♀. Not illustrated.

Dorsal bands as in ♂, slightly chitinized. Legs I and III as in ♂. ♂ genitalia asymmetric, especially in respect to the dilator, which, with the penis, is protruded from the body (as in Specimen 1). ♂ ventral plate invisible, but, as in the two foregoing specimens, there occurs a chitinous invagination of very irregular form and colour. Posterior end of abdomen asymmetric. Dorsal and ventral abdominal muscles as in ♂. *Internal organs:* three testes, two on the left side of normal size, one on the right much reduced.

(c) *With ♂ genitalia complete, the ♀ genitalia being represented by a unilateral gonopodial invagination.*

SPECIMEN 12, ♀. Pls. XII, XIII, XVI, fig. 2 and Text-fig. 8.

Deeply pigmented specimen. Dorsal bands fragmented (Pl. XII). Legs: pair I as in ♂ but modified. ♂ genitalia normal. ♂ ventral plate (Pl. XVI, fig. 2) divided in two separate portions of small size and irregular form. ♀ ventral plate small, irregular, to the left of it a small curved chitinous structure surrounded by several concentric ridges of the surface; this structure being a rudimentary gonopod which we term a gonopodial spot (*gon.s.*). The segment behind the ventral plate shows a corrugated surface. To the right of the ♂ and ♀ ventral plates there are three slightly chitinized areas. Dorsal abdominal muscles apparently as in ♂, the ventral as in ♀ *capitis* (Text-fig. 8). *Internal organs* (Pl. XIII): three testes (*t.*), two on the left side, widely apart, one on the right, all being pushed out of their normal position; vesicula seminalis (*v.sem.*) with accessory glands (*acc.gl.*) and ductus ejaculatorius (*d.ej.*) pushed into oblique position. The specimen shows, moreover, two large, completely formed ova (*ov.*) with opercula and micropyles, a portion of ovarial tube with young ovules, follicular and nutritive cells. The malposition of the ♂ sexual organs is attributable to pressure from the eggs which could not be expelled from the insect's body.



Text-fig. 8. *Pediculus humanus* race *capitis* ♀. Specimen 12 (also figured in Pls. XII, XIII, XVI, fig. 2). Cleared, showing certain abdominal muscles. (K. del.)

SPECIMEN 13, ♀. Pl. XIV.

Very pale specimen. Legs: pairs I and III as in ♂ but pair I somewhat modified. ♂ genitalia apparently normal. ♂ ventral plate entire, unpigmented. ♀ genitalia represented only by a unilateral invagination (*gon. invag.*) on the left side of the body in the form of a chitinized sack with sensory hairs inside. Dorsal and ventral abdominal muscles as in ♂. *Internal organs:* one small spherical testis (*t.*) on the right side, vesicula seminalis somewhat deformed and displaced by numerous eggs (*ov.*) of which 6 are well developed and show opercula with micropyles.

SPECIMEN 14, ♀. Pl. XVII, figs. 2, 3.

Well pigmented specimen. Dorsal bands as in ♂. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia apparently normal. ♂ ventral plate entire.

♀ genitalia represented only by a small chitinous plate or gonopodial spot (*gon.s.*) and close to it a deep invagination (*g.i.*) in the form of a curved tube the bottom of which is strongly chitinized and contains sensory hairs. Dorsal and ventral abdominal muscles as in ♂.

SPECIMEN 15, ♀. Pl. XVII, fig. 9.

Similar to Specimen 14, but possessing two gonopodial spots.

SPECIMEN 16, ♀. Pl. XVII, fig. 5.

Similar to Specimen 14, but the bottom of the gonopodial invagination situate beneath the ventral plate.

SPECIMEN 17, ♀. Pl. XVII, fig. 7.

Similar to Specimen 14, but leg-pair III with very reduced femoral spur. Gonopodial spots absent; tubular invagination is almost straight.

SPECIMEN 18, ♀. Not illustrated.

Slightly pigmented. Dorsal bands as in ♂. Legs: pair I as in ♂, pair III shrivelled but apparently of ♂ type. ♂ genitalia almost normal, slightly curved to the left. ♂ ventral plate very pale, entire, beneath it an oval invagination on the left side; this invagination contains sensory hairs. Dorsal and ventral abdominal muscles as in ♂.

Group II (14 ♀♂ specimens).

Posterior end of abdomen bilobed as in ♀. With ♀ genitalia well developed, ♂ genitalia obsolete or very much reduced and internal.

SPECIMEN 19, ♀♂. Text-figs. 9 A, 10 A.

Dorsal bands as in ♂. Legs: pair I as in ♂, pair III as in ♀. ♀ ventral plate with antero-lateral extensions (*ext.*). ♀ genitalia with gonopods normal. Dorsal abdominal muscles apparently as in ♂, partly macerated, ventral muscles as in ♀. Contains two eggs, one large.

SPECIMEN 20, ♀♂. Text-fig. 9 C.

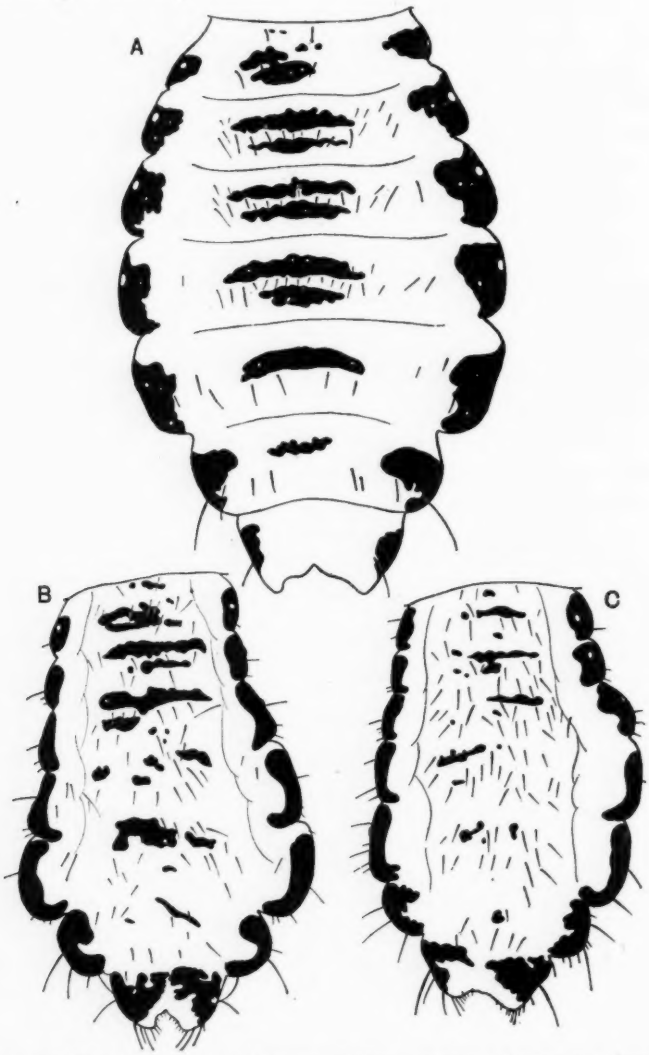
Dorsal bands fragmented, very small pieces. Legs: pairs I and III as in ♀, leg III with moderate femoral spur. ♀ ventral plate normal. Gonopods normal. Contains one large egg.

SPECIMEN 21, ♀♂. Not illustrated.

Much like Specimen 19, but leg I of intermediate form and leg III as in normal ♀.

SPECIMEN 22, ♀. Text-figs. 9 B, 10 E.

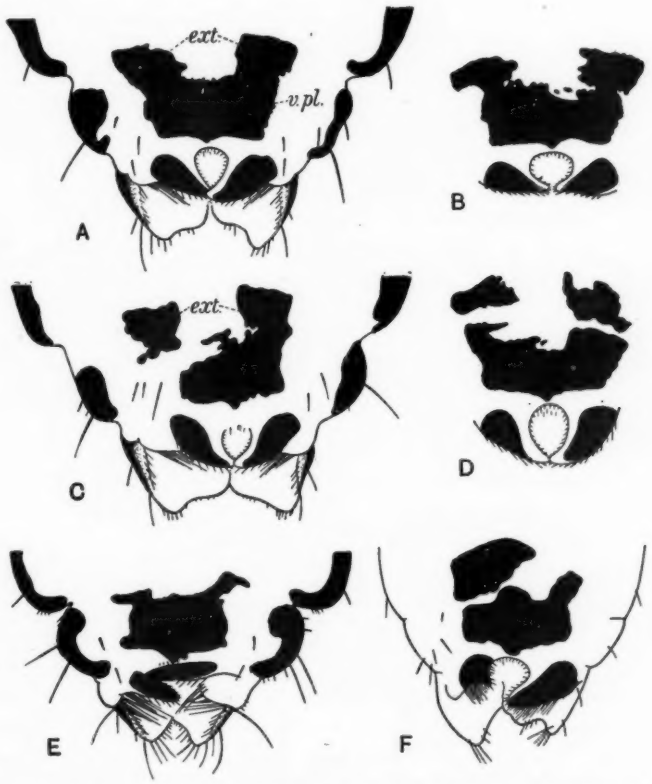
Dorsal bands fragmented and irregular. Legs: pair I of intermediate form, pair III as in ♀. ♀ ventral plate irregular, with small antero-lateral extensions. Gonopods normal (displaced by contraction as figured). Contains one large egg extending to thorax.



Text-fig. 9. *Pediculus humanus* ♀. Abdomens of three specimens showing the dorsal bands. (A) Specimen 19, *corporis*, the same as in Text-fig. 10 A. (B) Specimen 22, *capitis*, with fragmented dorsal bands, the same as in Text-fig. 10 E. (C) Specimen 20, *capitis*, with dorsal bands much fragmented and reduced. (N. del.)

SPECIMEN 23, ♀. Not illustrated.

Dorsal bands as in ♂, complete. Legs: pair I as in ♂, pair III as in ♀. ♀ ventral plate very large, bearing perforations anteriorly. Gonopods normal, strongly chitinized. Abdominal muscles: dorsally as in ♂, ventrally as in ♀.



Text-fig. 10. *Pediculus humanus* ♀. Posterior portion of abdomen, ventral aspect, showing ventral plate (*v.pl.*) with its antero-lateral extensions (*ext.*) at times separated. (A) Specimen 19 (same as in Text-fig. 9 A); (B) Specimen 25; (C) Specimen 28; (D) Specimen 30; (E) Specimen 22 (same as in Text-fig. 9 B); (F) Specimen 29, showing asymmetric gonopods and posterior abdominal lobes, (E) being *capitis*, the rest *corporis*. (N. del.)

SPECIMEN 24, ♀. Not illustrated.

Dorsal bands as in ♂, complete. Legs: pair I as in ♂, pair III as in ♀. ♀ ventral plate well developed, with antero-lateral extensions having crenate borders. Gonopods normal. Posterior abdominal lobes much reduced and only visible dorsally. Dorsal abdominal muscles macerated, but apparently as in ♀, ventral muscles as in ♀.

SPECIMEN 25, ♀. Text-fig. 10 B.

Dorsal bands much as in Specimen 19. Legs: pair I as in ♂, pair III as in ♀. ♀ ventral plate with each antero-lateral extension united to plate by a narrow neck. Dorsal abdominal muscles as in ♂, ventral muscles macerated.

Text-fig. 11. *Pediculus humanus* race *corporis* ♀. Specimen 26, showing chitinous invagination with sensory hairs in the last abdominal segment. See Pl. XVII, fig. 8 for details of this structure. (K. & N. del.)

SPECIMEN 26, ♀. Text-fig. 11 and Pl. XVII, fig. 8.

Dorsal bands as in ♂. ♀ ventral plate, etc., as in Specimen 25, leg III bearing but a slight femoral spur. Ventral abdominal muscles as in ♀. This specimen shows a small chitinous sack containing sensory hairs; the sack, situated on the left side in the last abdominal segment, is only visible by transparency from the dorsal side.

SPECIMEN 27, ♀. Not illustrated.

Similar to Specimen 26, but pale. Contains three eggs, one with operculum facing vulva, one transverse.

SPECIMEN 28, ♀. Text-fig. 10 C.

Similar to Specimen 19, but the ventral plate of peculiar form, with left antero-lateral extension united to it, the right extension forming a separate plate.

SPECIMEN 29, ♀. Text-fig. 10 F.

Dorsal bands as in normal ♂. Legs: pair I as in ♂, pair III as in ♀. The whole posterior part of abdomen asymmetric. Ventral plate with left antero-lateral extension moderate, the right one forming a separate plate. Left gonopod normal, right gonopod very much reduced although bordered by sensory hairs. Posterior abdominal lobes abnormal, the left being short and indented. Abdominal muscles: dorsally as in ♂, ventrally as in ♀.

SPECIMEN 30, ♀. Text-fig. 10 D.

Resembling Specimen 19, but with ventral plate having its anterior border ragged; the antero-lateral extensions form two separate plates. Dorsal abdominal muscles as in ♂.

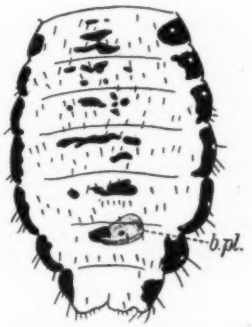
SPECIMEN 31, ♀. Text-fig. 12.

Dorsal bands fragmented. Legs: pair I lost, pair III as in ♀. Ventral plate more regular than in Specimen 30, the antero-lateral extensions similarly separated. Gonopods normal. Posterior abdominal lobes truncated, slightly irregular. Abdominal muscles: dorsally as in ♂, ventrally as in ♀. *Internal*

organs: viewed dorsally by transparency, the specimen shows structures resembling a rudimentary basal plate and vesica penis; one left testis is well developed, young ovules are present.

SPECIMEN 32, ♀. Not illustrated.

Resembles Specimen 31 in some respects. Dorsal bands complete, broad. Legs: pair I as in ♂, pair III as in ♀. Ventral plate with one antero-lateral extension forming a separate plate, the other united by a very narrow neck (recalling Specimen 28 shown in Text-figure 10 c). Posterior abdominal lobes truncated, asymmetric, the left lobe being much reduced. Abdominal muscles: dorsally as in ♂, ventrally as in ♂ but the second set of muscles incomplete. *Internal organs:* one large testis filled with spermatozoa, young ovarial tubes, their relations obscurely visible. A sub-gonopodial prolapse is present; it consists of basal plate, dilator, penis and vesica penis, all distorted and reduced; this complex doubtless corresponds to the rudimentary ♂ genitalia which are contained inside the body of Specimen 31.



Text-fig. 12. *Pediculus humanus* ♂. Specimen 31. Abdomen in dorsal aspect, showing fragmented dorsal bands and ♂ genitalia (*b.pl.* = basal plate), the latter seen by transparency. (K. & N. del.)

DESCRIPTION OF BACOT'S 123 HERMAPHRODITES: MATERIAL (c).

This material contained males, females, and 123 hermaphrodites, derived from various crosses between *capitis* and *corporis* (see Table on p. 315) as follows:

Cross I. *Corporis* ♂ × *capitis* ♀: the 3 generations F_1, F_2, F_3 contained no hermaphrodites, the males predominated over the females.

Cross II. *Capitis* ♂ × *corporis* ♀: the 3 generations F_1, F_2, F_3 contained 1 *hermaphrodite* (Specimen 33), the proportion of the sexes in this case being also abnormal, there being more males than females.

SPECIMEN 33. *Of* ♀ *type*, very pale. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia asymmetric, with protruded penis; on the ventral side in the median line there is a large invaginated chitinous mass with sensory hairs, this representing the vagina and gonopods of ♀. Muscles invisible. *Internal organs:* a distorted vesicula seminalis; testes and ovules present, but it is difficult to determine their number and to define their contours.

Cross III. *Capitis* ♂ × *corporis* ♀: yielded but one generation, F_1, with very few specimens and no hermaphrodites.

Cross IV. *Capitis* ♂ × *corporis* ♀: yielded but one generation, F_1, comprising males and females in equal numbers (43: 43) and 5 *hermaphrodites*.

SPECIMENS 34–38 are all *of* ♀ *type* and have ♂ and ♀ genitalia more or less developed, legs I and III being of ♂ and ♀ type respectively. Only one example, No. 34, presented an extruded vesica penis, the basal plate and dilator being deformed; there are two gonopods, a ♀ ventral plate and a prolapse beneath the gonopods. No. 35 showed a medio-ventral bladder-like prolapse bearing sensory hairs and rudimentary gonopods with their component parts widely separated; the specimen also showed two testes filled with spermatozoa, likewise some eggs. Nos. 36–38 had median or lateral invaginations of the ♀ genitalia, these forming irregular sacks bearing sensory hairs. The dorsal bands, when clearly visible through being pigmented, were fragmented.

Cross V. *Capitis* ♂ × *corporis* ♀: yielded but one generation composed of 75 ♂♂, 26 ♀♀, 7 *hermaphrodites* and one specimen with abnormal legs (see pp. 319, 320); the ♂♂ predominate (69 per cent.).

SPECIMENS 39–45. But one hermaphrodite, No. 39, is *of* ♀ *type*, its ♀ characters consisting in the structure of leg III, the presence of lateral ventral invaginations representing the rudiments of ♀ genitalia. Nos. 40–45 are *of* ♀ *type* with gonopods and posterior abdominal lobes, their hermaphroditic characters being evident because (*a*) some have fragmented dorsal bands, (*b*) leg-pair I in almost all is of ♂ type, (*c*) in two the posterior abdominal lobes are asymmetrical and bifurcated, (*d*) the rudiments of ♂ genitalia are represented by more or less regular chitinous invaginations some of which are situate in the posterior lobes, others being in the penultimate abdominal segment; in one case the vesica penis is more developed and protruded. *Internal organs:* eggs are present in nearly all the hermaphrodites, one containing about 10 well developed operculated eggs besides a left testis with spermatozoa.

Cross VI. *Capitis* ♂ × *corporis* ♀: yielded three generations composed of 693 ♂♂, 167 ♀♀, and 110 *hermaphrodites*, their proportions being respectively 71, 17 and 12 per cent. The first generation of this cross (F_1), contains 128 ♂♂, 16 ♀♀, all normal. Four pairs (♂♀) of the F_1 generation produced 4 families (F_2 generation), denoted by the letters *K*, *L*, *M*, *N*, which we shall consider separately as follows:

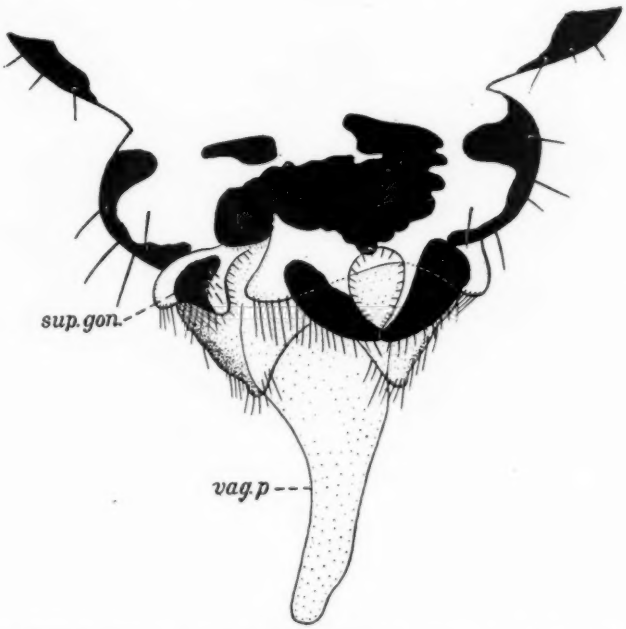
Family *K* (F_2 generation).

This family consists of 104 ♂♂, 2 ♀♀ and 20 *hermaphrodites*.

SPECIMENS 46–47, that is 2 examples, are *of* ♀ *type* with ♂ characters limited to fragmented dorsal bands and the structure of leg I. No. 46 is devoid of interest, but not so No. 47 (Text-fig. 13), with dorsal bands apparently slightly fragmented (obscured because gorged with blood). Legs: pair I as in ♂, pair III as in ♀. The peculiarity of this example consists in

the presence of a small *supplementary gonopod* on the right side which displaces the otherwise normal gonopods to the left. The specimen contains a large number of eggs and shows a vaginal prolapse.

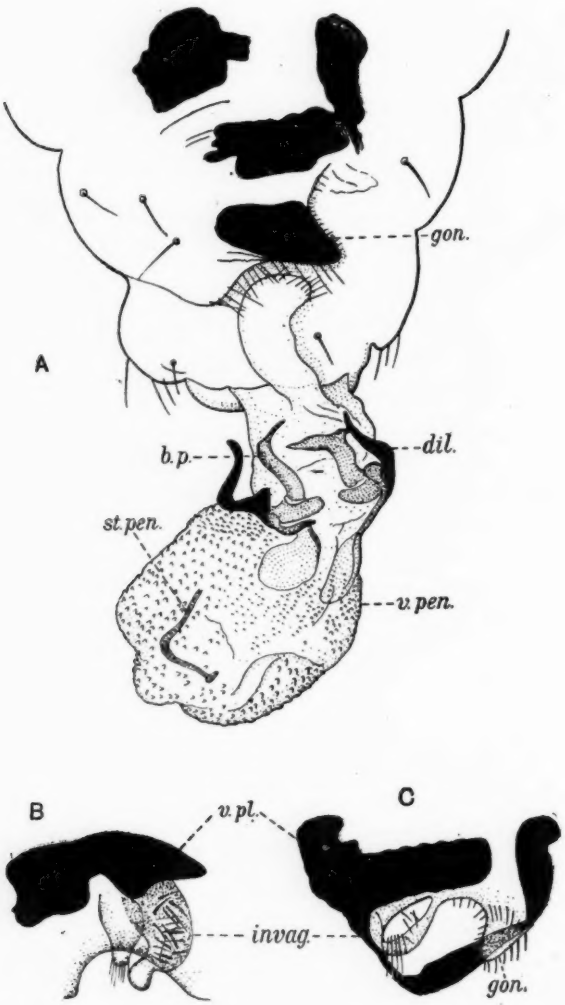
SPECIMENS 48–65, that is 18 examples, are *of ♀ type* and show ♀ characters to a varying degree as follows: (*a*) No. 48 has gonopods of normal form and size. (*b*) No. 49 (Text-fig. 14 C) has one sub-normal gonopod, the other being invaginated; the gonopods are surrounded by a chitinous band originating from the ♀ ventral plate, this almost annular structure serving to explain the abnormality of the ♀ genitalia in Specimen 7 (p. 287). (*c*) Nos.



Text-fig. 13. *Pediculus humanus*, cross between *capitis* and *corporis*, ♀. Specimen 47. Posterior portion of abdomen, ventral aspect, showing supplementary gonopod (*sup. gon.*) and vaginal prolapse (*vag. p.*). (K. & N. del.)

50–65 have the ♀ genitalia represented by unilateral, bilateral, or median invaginated structures of irregular form bearing sensory hairs (Text-fig. 14 B, being Specimen 50). In some specimens, for example Nos. 51–52 (Text-fig. 15 A and B), one part of the ♀ genitalia, representing the external organs, is invaginated in the form of a darkly pigmented and heavily chitinized mass, the other part, representing the vagina, is extruded in the form of a vesicle. The ♂ genitalia in all of these 18 examples are more or less deformed; two specimens show the vesica penis protruded, in one it is reduced, whilst

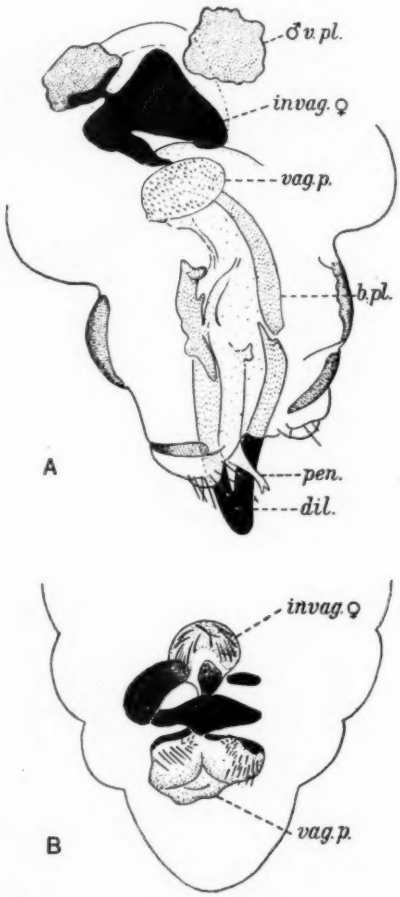
in the other (No. 53, see Text-fig. 14 A) it is of normal size with the basal plate much reduced, the dilator divided in two pieces, the penis being absent; this specimen shows but one gonopod.



Text-fig. 14. *Pediculus humanus*, cross between *capitis* and *corporis*. (A) Specimen 53, ♀, showing extruded ♂ genitalia; lettering as in Text-figs. 17, 20. (B) Specimen 50, ♀, detail showing ♂ ventral plate (*v.pl.*) and two invaginated structures with sensory hairs and posterior part protruding. (C) Specimen 49, ♀, showing two gonopods, one abnormal, surrounded by deformed ventral plate. (K. & N. del.)

Family *L* ($\dot{F}_2$ generation).

This family consists of 82 ♂♂, 17 ♀♀ and 31 *hermaphrodites*. The latter may be classified in three groups, (*a*) of ♀, (*b*) of ♂, (*c*) of intermediate type between ♂ and ♀:

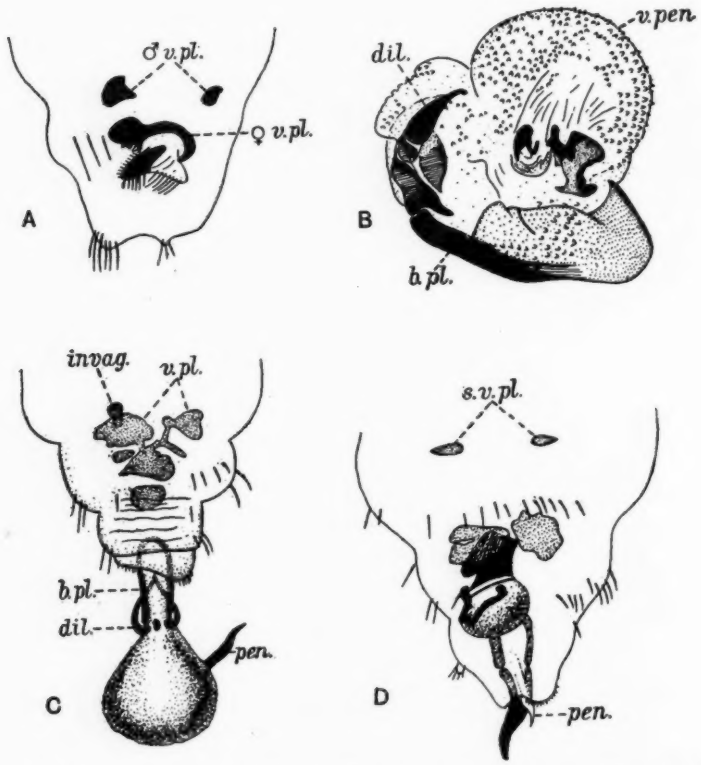


Text-fig. 15. *Pedicutus humanus*, cross between *capitis* and *corporis*. Specimens 51-52, ♀, F_2 generation, showing posterior end of abdomen in two examples (A) and (B). The ♀ genitalia reduced, deformed, partly invaginated, the vagina prolapsed. (K. & N. del.)

(*a*) SPECIMENS 66–81 *of* ♀ *type*. The 16 specimens with gonopods, posterior abdominal lobes and ♀ ventral plate well developed. The ♂ characters consist of more or less fragmented dorsal bands, the structure of leg I, the ♂ ventral plate; this plate, in some cases, consists of two fragments of variable

size and separated from the ♀ plate or fused with it to form its lateral extension (compare with Text-fig. 10).

(*b*) SPECIMENS 82–94 *of* ♀ *type.* The 13 specimens with ♂ genitalia more or less developed, but two examples being of interest in showing the

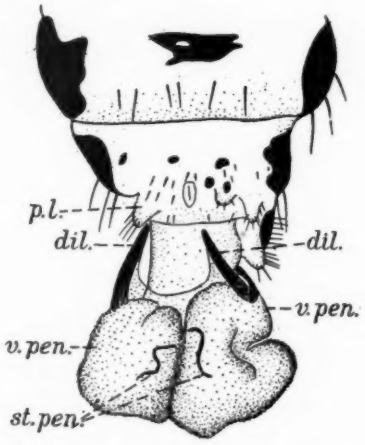


Text-fig. 16. *Pediculus humanus*, cross between *capitis* and *corporis*, illustrating parts of 3 specimens of the F_2 generation. (A) Specimen 95, hermaphrodite of intermediate type between ♀ and ♂, posterior end of body showing ♂ ventral plates, and ♀ ventral plate surrounding a single gonopod and its basal portion. (B) Specimen 95 (as before), reduced and deformed ♂ genitalia extracted from the body. (C) Specimen 82, showing protruded ♂ genitalia with basal plate and dilator reduced. (D) Specimen 84, showing much deformity and reduction of ♀ genitalia, also supplementary ventral plates (*s.v.pl.*). (K. & N. del.)

vesica penis extruded. No. 82 (Text-fig. 16 c), of a form intermediate between *capitis* and *corporis*, is fairly dark, with dorsal bands normal, leg I as in ♂, leg III as in ♀; statumen penis and penis fairly normal, basilar plate and dilator reduced and almost extruded from the body; the ♂ and ♀ ventral plates form an irregular complex.

No. 83 (Text-fig. 17), a very dark specimen. Dorsal bands normal, as in the ♂. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia extruded as in copulation, of very peculiar structure; the *vesica penis bilobed*, each lobe being connected with a lateral portion of the dilator, which, instead of ending in a point, consists of two widely separated rami (resembling somewhat No. 53). The statumen penis is duplicated, but the penis is absent. The ♂ ventral plate is divided in two pieces between which occurs a very dark chitinous invagination representing rudimentary ♀ genitalia.

The hermaphroditic characters of this group (*b*) consist of fragmented dorsal bands, the ♀ structure of leg III, the presence of a ♀ ventral plate though deformed and invaginated, internal chitinous invaginations with sensory hairs, and various forms of prolapsed vagina. In a few examples of groups (*a*) and (*b*) we observe two very *small supplementary chitinized plates*



Text-fig. 17. *Pediculus humanus*, cross between *capitis* and *corporis*. Specimen 83, ♀, showing posterior end of abdomen, dorsal aspect, with protruded double vesica penis (*v.pen.*), dilator (*dil.*), posterior abdominal lobes (*p.l.*), statumen penis (*st.pen.*). (K. & N. del.)

situate ventrally in the segment anterior to that which normally bears the ventral plate (No. 84, see Text-fig. 16 D).

(*c*) SPECIMENS 95–96 *of intermediate type* between ♀ and ♂.

No. 95 (Text-fig. 16 A and B) has the dorsal bands slightly fragmented, leg I as in ♂, leg III as in ♀. The posterior end of abdomen asymmetrical and of intermediate type with abdominal lobes much reduced. ♂ ventral plate consists of two widely separated pieces. ♀ ventral plate of annular form, surrounding a gonopod with its basal portion. ♂ genitalia with basal plate, dilator, vesica penis, and statumen penis, all reduced, deformed, and completely enclosed in the last abdominal segment.

No. 96 differs from the foregoing in having complete dorsal bands and two gonopods, the ♀ ventral plate not being annular.

Family *M* (F_2 generation).

This family consists of 19 ♂♂, 28 ♀♀ and 10 *hermaphrodites*.

SPECIMENS 97–98, 2 examples, are *of* ♀ *type* with gonopods and posterior abdominal lobes well developed; the ♂ characters being reduced to fragmented dorsal bands, the structure of leg I, and, in one specimen, the bipartite ♂ ventral plate.

SPECIMENS 99–106, 8 examples, are *of* ♀ *type*, with ♂ genitalia slightly or much deformed. The ♂ ventral plate varies in shape, but in most cases is bipartite. The ♀ characters of these specimens are: the ♀ structure of leg III; the ♀ genitalia, only well developed in one case, are reduced in the others to a simple or multiple invagination of very irregular shape and bearing sensory hairs; in a few cases there is also a slight devagination which represents the prolapsed vagina. One specimen shows protruded ♂ genitalia of irregular form.

Family *N* (F_2 generation).

This family consists of 92 ♂♂, 7 ♀♀ and 10 *hermaphrodites*.

SPECIMENS 107–114, 8 examples, are *of* ♀ *type* with posterior abdominal lobes and gonopods well developed; the ♂ characters are: dorsal bands complete, fragmented, or reduced to a few chitinized spots, the ♂ structure of leg I, and the lateral extensions to the ♀ ventral plate. One of these specimens is of special interest:

No. 114 (Text-fig. 18): with the general appearance of a ♀. The sole ♂ character, visible externally, consists in the much fragmented and reduced dorsal bands. The abdomen contains many *eggs of which one shows a completely formed embryo*. As the specimen was dried and shrivelled, and had to be treated with caustic potash prior to examination, the only parts of the embryo which are visible by transparency are the claws of its three pair of legs.

The embryo had therefore undergone complete development within the female's body. There is no reason to suppose that the embryo was produced parthenogenetically, because the female appears to be normal and emanates from a lot comprising males. Moreover, large numbers of virgin females raised in our laboratory, whilst ovipositing normally, never produced parthenogenetic offspring (see Nuttall, *Parasitology*, x. p. 141). The only plausible explanation of the phenomenon is that the internal genitalia of this female were sufficiently normal for copulation to take place, but that they presented some malformation which impeded oviposition. The egg, having been fertilized, remained imprisoned in the female and the embryo underwent complete development *in situ*. There is nothing surprising in this occurrence,

for several cases are known of accidental viviparity in oviparous insects. As instances we may cite the observations of Lowne (1895) on *Calliphora*, Roubaud (1909) on *Pycnosoma*, Guyénot (1913) on *Drosophila*, Keilin (1916) on *Aphiochaeta*, *Phora*, *Calliphora* and *Mucsa*[1].

SPECIMENS 115–116, 2 examples, are *of* ♀ *type*, and sexually non-functional.

No. 115 is fairly dark, with dorsal bands complete, leg I as in ♂, leg III as in ♀. ♂ genitalia reduced, deformed, completely imprisoned in the body. ♂ ventral plate bipartite. ♀ genitalia invaginated and strongly chitinized. Posterior end of body irregularly truncate.

Text-fig. 18. *Pediculus humanus*, cross between *capitis* and *corporis*. Specimen 114, ♀. Abdomen, with outline of eggs, viewed by transparency, one egg containing a fully developed larva as seen by the claws (*cl.*). (N. del.)

No. 116 with dorsal bands slightly fragmented, legs as in No. 115. ♂ genitalia completely imprisoned, reduced, deformed. ♀ genitalia invaginated, consisting of irregular, strongly chitinized structures. Posterior end of abdomen rounded as in ♂.

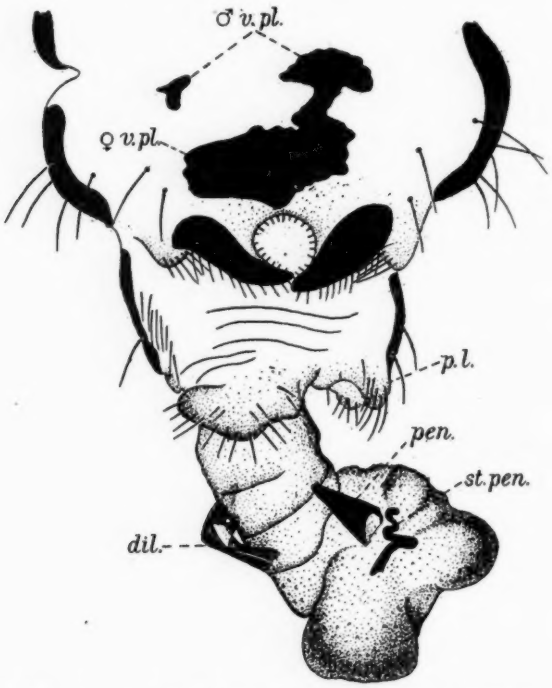
[1] Consult Keilin, D. (1916). "Sur la viviparité chez les diptères et sur les larves de diptères vivipares." *Arch. zool. expér. et gén.* LV. 393–415 (contains bibliography).

The F_3 generation of Cross VI (see p. 316) comprising families *O–S*.

Family *O* (F_3 generation).

This family consists of 22 ♂♂, 9 ♀♀ and 5 *hermaphrodites*.

SPECIMEN 117 is the only one *of* ♀♂ *type*, with posterior abdominal lobes and gonopods, the left gonopod and its basilar part is elongated, the posterior border being rectilinear; this gonopod occupies a median position, whilst the right gonopod is displaced laterally. The ♂ characters consist of reduced and fragmented dorsal bands, the ♂ structure of leg I; one half of the bipartite ♂ ventral plate is fused with the ♀ plate, the other half being free.



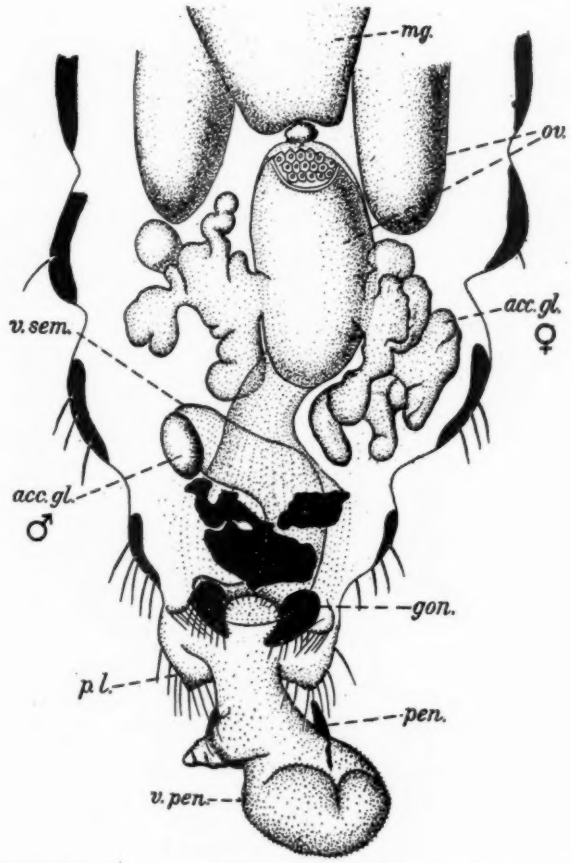
Text-fig. 19. *Pediculus humanus*, cross between *capitis* and *corporis*. Specimen 118, of intermediate type between ♀♂ and ♂♀. Of F_3 generation, showing ♂ genitalia extruded, the ♀ genitalia being fairly complete. (K. del.)

SPECIMENS 118–119, two examples, are *of intermediate type* between ♀♂ and ♂♀:

No. 118 (Text-fig. 19). With dorsal bands invisible, leg I as in ♂, leg III as in ♀. ♂ genitalia extruded together with the reduced basal plate and dilator; vesica penis well developed, penis abnormally broad, statumen penis crumpled. ♂ ventral plate bipartite, the right part reduced to an isolated

fragment, whilst the left part is fused with the ♀ plate to form its lateral extension. Gonopods normal. Posterior abdominal lobes reduced.

No. 119 (Text-fig. 20) resembles the foregoing but is of special interest. Dorsal bands invisible. Legs: pair I as in ♂, pair III as in ♀. ♂ genitalia in

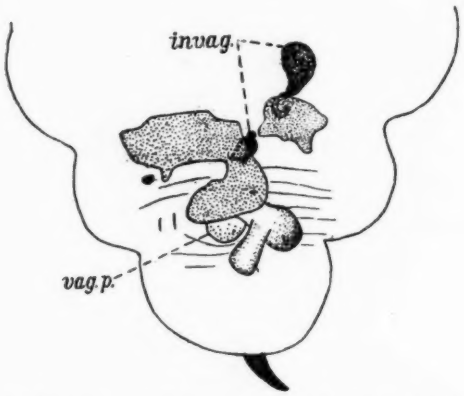


Text-fig. 20. *Pediculus humanus*, cross between *capitis* and *corporis*. Specimen 119, of intermediate type between ♀ and ♂. Posterior half of abdomen, ventral aspect, external and internal structure seen by transparency. Midgut (*mg.*), ova (*ov.*), accessory gland of ♀ (*acc.gl.*♀), gonopods (*gon.*), posterior abdominal lobes of ♀ (*p.l.*), vesicula seminalis (*v.sem.*), accessory gland of ♂ (*acc.gl.*♂), penis (*pen.*). (K. del.)

the form of an extruded sack, reduced in size, but bearing a strongly chitinized penis; dilator apparently obsolete. Posterior lobes as in ♀. Gonopods normal. ♀ ventral plate slightly irregular. ♂ ventral plate in two distinct pieces of irregular form, situate near the ♀ ventral plate. Dorsal abdominal muscles

as in ♂, ventral muscles invisible. *Internal organs:* vagina and uterus of normal structure, the uterus containing a large operculated egg and connected laterally with two well developed accessory glands; a few other large eggs occupy the abdomen. Dorsally to the vagina is seen a large vesicula seminalis of abnormal shape (compare Text-figs. 20 and 1 on p. 281). *The specimen appears to occupy an intermediate position between our specimens included under Group I and Group II respectively* (see p. 286).

SPECIMENS 120–121 *of ♀♂ type* have the ♀ characters represented by the structure of leg III and the ♀ genitalia which, in No. 120, are reduced to three chitinous invaginations with sensory hairs, in No. 121, to a polypoid mass spread across the segment. These specimens are of interest because of the presence on them of hypertrophied peribuccal hairs which are described on pp. 322–323 and shown in Text-fig. 28.



Text-fig. 21. *Pediculus humanus*, cross between *capitis* and *corporis*. Specimen 136, ♀♂, of the F_3 generation, posterior end of abdomen with rudiments of ♀ genitalia partly invaginated, partly evaginated. (K. del.)

Family *P* (F_3 generation).

This family consists of 16 ♂♂, 31 ♀♀ and 15 *hermaphrodites*.

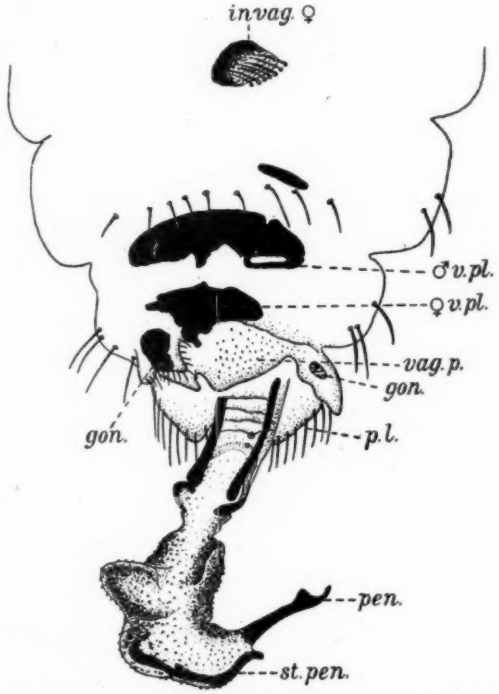
SPECIMENS 122–130, namely 9 examples, are *of ♀♂ type*, the ♂ characters being the ♂ structure of leg I, the dorsal bands, these being fragmented and in some cases reduced to two or three spots. Some of the specimens contain two to four operculated eggs.

SPECIMENS 131–136, namely 6 specimens, are *of ♀♂ type* with ♀ characters comprised in the structure of leg III. The ♀ genitalia are reduced to variously devaginated or invaginated structures (Text-fig. 21).

Family *Q* (F_3 generation).

This family consists of 100 ♂♂, 17 ♀♀ and 13 *hermaphrodites*.

SPECIMENS 137–138, namely 2 examples, are *of ♀ type* with ♂ characters consisting of fragmented dorsal bands and the ♂ structure of leg I; one specimen has a bipartite ♂ ventral plate, the posterior abdominal lobes showing several irregular protrusions.



Text-fig. 22. *Pediculus humanus*, cross between *capitis* and *corporis*. Specimen 149, of intermediate type between ♀ and ♂, F_3 generation, with reduced gonopods, prolapsed vagina and protruded ♂ genitalia. (K. & N. del.)

SPECIMENS 139–148, namely 10 examples, are *of ♀ type* with ♀ characters comprised in the ♀ structure of leg III and the more or less rudimentary ♀ genitalia in the form of unilateral, bilateral, or median invaginated or evaginated structures bearing sensory hairs.

SPECIMEN 149 (Text-fig. 22) is of interest in being *of intermediate type* between ♀ and ♂ and showing a protruded vesica penis. Dorsal bands normal, leg I as in ♂, leg III with very small femoral spur. Dilator and basal plate protruded with vesica penis which bears a normal penis and statumen penis. The ♂ ventral plate is normal, separate from the reduced ♀ plate. The rudi-

mentary gonopods are widely apart with the prolapsed vagina filling the interspace, whilst the posterior abdominal lobes appear normal. Anterior to the ♂ ventral plate there is a chitinous invaginated sack with sensory hairs (*invag.* ♀), the sack undoubtedly representing a part of the ♀ genitalia. *Internal organs:* two testes were observed on the left side, being apparently fused, also a small testis on the right side.

Family *R* (F_3 generation).

This family consists of 52 ♂♂, 8 ♀♀ and 2 *hermaphrodites*.

SPECIMENS 150–151. Both *of* ♀ *type*.

No. 150 has fragmented dorsal bands, leg I as in ♂, leg III as in ♀. ♂ genitalia complete, with dilator end and penis protruded; ♂ ventral plate bipartite and reduced to a small spot on the right side whilst fused with the ♀ plate on the left side to form a very large lateral extension. Gonopods normal.

No. 151 shows no ♀ genitalia; the ♂ genitalia are distorted and imprisoned in the body.

Family *S* (F_3 generation).

This family consists of 7 ♂♂, 32 ♀♀ and 4 *hermaphrodites*.

SPECIMENS 152–153, namely 2 examples, are *of* ♀ *type* with ♂ characters represented by dorsal bands and the structure of leg I. The posterior abdominal lobes are of irregular shape.

SPECIMENS 154–155, 2 examples, are *of* ♀ *type* with ♂ genitalia more or less normal, the ♀ characters being the form of leg III and the invaginated remains of ♀ genitalia.

GENERAL CHARACTERS OF HERMAPHRODITES IN *P. HUMANUS*.

In considering the general character of the hermaphrodites we shall commence by dwelling upon certain parts of their anatomy that have undergone special modifications consequent upon the condition of hermaphroditism. The various structures, for convenience sake, are considered in the following sequence:

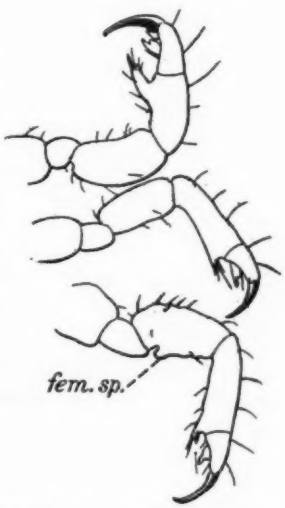
Dorsal bands.

Dorsal bands, normally, only occur in males (Text-fig. 2), although they are not always distinct. Thus, in unpigmented specimens, they can only be discerned if viewed by reflected light, when they appear as smooth glossy areas upon the otherwise rugose surface of the dorsal side of the abdomen. In well pigmented hermaphrodites the bands may have a normal structure, being complete, or they may be either frayed, fused, or fragmented (Text-figs. 9, 12, 6). In the latter case, the fragments may be of irregular form and of very

unequal size, being scattered upon the back of the abdomen. At times the fragments are reduced to but two or three minute chitinous spots, in which case other characters which distinguish hermaphrodites indicate that the spots actually represent rudiments of dorsal bands. The bands are generally complete in hermaphrodites of predominantly male character and are fragmented in those with predominantly female character, but there are numerous exceptions, as exemplified, for instance, in Plate XII, where an hermaphrodite having male characters is shown with fragmented bands; similarly, hermaphrodites with predominantly female characters may at times have bands complete (Text-fig. 9 A). In no case did we find a specimen with the bands developed merely on one side.

Legs.

Most hermaphrodites show the characters of both sexes in their leg structure, the first pair being of male type, the third of female type (Text-fig. 23). It follows that in copulation these legs may function normally, either as in the male or female respectively. In all cases the structure of the corresponding legs on both sides is identical.



Text-fig. 23. *Pediculus humanus*, cross between *capitis* and *corporis*, ♀, the 3 legs of one side showing ♂ character of leg I, and ♀ character of leg III which consists in the presence of a femoral spur (*fem.sp.*). (N. del.)

Longitudinal muscles of abdomen.

In hermaphrodites of predominantly ♂ character, the dorsal and ventral muscles running longitudinally from segment to segment are generally of male type, but exceptions occur wherein the ventral muscles are of female type or even more reduced than in the normal female. In hermaphrodites of female type the dorsal muscles are usually of male character and the ventral muscles as in the female; exceptions occur, however, in which the muscles of both sides are as in the normal female.

Ventral plates of male and female.

The ventral plates in hermaphrodites vary greatly in their structure and relations to each other. Thus (1) the ♂ plate may be present alone and be of normal form; (2) the ♂ plate may be normal and the ♀ plate reduced and partly invaginated; (3) the ♂ and ♀ plates may coexist and both be normal in shape; (4) the ♂ plate may be bipartite and the ♀ plate normal; (5) a half of the bipartite ♂ plate may be free, the other half being fused to the ♀ plate to form what we term its antero-lateral extension; (6) the two halves of the ♂ plate may be fused with

the ♀ plate which thereby acquires symmetrical lateral extensions; (7) the extensions vary in size down to their complete disappearance, leaving the ♀ plate alone. The form of the several plates may be regular, asymmetrical, or the margins may be frayed[1].

Genital organs.

(A) *The external genitalia.*

The large number of hermaphrodites (155) examined by us has yielded a complete series of gradations in which the external genitalia of both sexes coexist and occur in varying proportions. This gradation is rendered clear by the following grouping:

Group	♂ Armature	♀ Armature
1	Complete	Absent*
2	,,	Represented by gonopodial spots or internal sacks, lobes absent†
3	,,	Rudimentary gonopods, uni- or bilateral, lobes absent
4	,,	Complete but reduced, lobes absent
5	,,	Complete, lobes absent
6	Complete but deformed	,, ,, ,,
7	Reduced and deformed	,, ,, rudimentary
8	,, ,, ,,	,, ,, present
9	Reduced to an invaginated sack or completely internal, or reduced to an internal sack	Complete in all respects
10	Absent*	Complete in all respects

* But the hermaphrodite character was indicated by the presence of dorsal bands and the structure of legs I and III, or by internal genital organs.

† By "lobes," for brevity sake, are meant the posterior abdominal lobes that characterize the ♀.

The fairly frequent coexistence of the two sexual armatures in an almost complete form is probably explained by the circumstance that the points of origin (Anlagen) of the two sets of organs are slightly separated; consequently the armatures, during their development, do not intrude on each other.

The *invaginations*, occurring commonly in hermaphrodites of *Pediculus*, represent parts of the external genitalia, either ♂ or ♀. To understand the origin of the invaginations, it should be remembered that the genital armature is rapidly formed during the last larval stage, its development commencing with an intense proliferation inward of the hypoderm. Immediately before the last moult, the newly formed genitalia appear more or less folded beneath the larval cuticle, but, when the insect moults, these organs acquire their definite form. If we assume that the proliferation of the hypoderm, for

[1] Curiously enough the male ventral plate in *Pediculus* appears to have escaped notice hitherto although it is a striking feature. This is doubtless due to previous observers not having studied well pigmented specimens where the plate is most in evidence. The plate serves for the origin of the retractor muscles of the male copulatory apparatus.

some reason, does not take place uniformly, we can understand why the organs that are formed in the folds of the developing tissue may not expand to their normal form and remain imprisoned within the body of the insect. The simultaneous growth of the organs of both sexes in a hermaphrodite suffices to explain these irregularities of proliferation.

The *devaginations*, frequently observed by us in the hermaphrodites, differ according to the character of the specimen. In *female* organs two kinds of devaginations occur, (*a*) natural devagination due to malformation in the course of development, (*b*) traumatic devaginations or prolapses, which we attribute to injury during coitus, this, at times, leading to rupture of the vagina followed by expulsion of the internal genital organs. In *male* organs we have to consider what takes place normally. In *Pediculus*, and certainly in some other Anoplura, the male genital armature is retracted into the body when at rest, but becomes extruded in the form of a sack surmounted by a penis during copulation. In Bacot's material, we found a number of hermaphrodites that had died with their male genitalia extruded, this being attributable to one of three causes: (*a*) the sack having been extruded during ecdysis and the atrophied retractor muscles not permitting of its retraction, (*b*) the sack having been extruded during coitus and not having been retracted for the reason just stated, (*c*) the sack having been extruded owing to the pressure exerted by the proliferation of the female genital organs. The last explanation appears inadequate to us because we have seen specimens replete with eggs (Specimen 13, Pl. XIV) in which the male genitalia are not extruded. Whatever the cause of the extrusion may be, the inability to retract the sack (vesica penis) is certainly due to atrophy of the retractor muscles, which in all such cases are correlated with an atrophic condition of the basal plate upon which the retractors are inserted.

In no case were the male and female genitalia situated to the right or left of each other as in halved or lateral gynandromorphs.

(B) *Internal sexual organs.*

The state of preservation of the material studied only permitted us to examine the internal organs in twelve specimens. These, however, showed certain variations in the degree of development attained by the male and female organs of which the following may serve as examples:

(1) A ♀ contains 4 well developed testes, the remaining male organs being normal. There are also two large eggs present, but they have no means of exit from the body.

(2) A ♀ (Specimen 12, Pl. XIII, described on p. 290) contains 3 testes widely apart, with all the other male organs normal and but slightly displaced. Two large eggs and some young ovules are present but have no means of exit from the body, the secondary female sexual organs being obsolete.

(3) A ♀ (Specimen 13, Pl. XIV, described on p. 290) contains 1 testis,

the other male organs being almost normal. Several large eggs are present, but they have no means of exit because all the other female organs are reduced to a small chitinous sack containing sensory hairs.

(4) An hermaphrodite of intermediate type between ♀ and ♂ (Specimen 119, Text-fig. 20, described on p. 305) has all the female internal sexual organs complete, also of the male organs, a lateral half of the vesicula seminalis with its accessory gland, a rudimentary vesica penis and penis, but no testes.

(5) Several ♂ (for example, Specimen 31, Text-fig. 12, described on p. 294) have the female genital organs complete besides 1 or 2 testes, there being no further traces of male organs.

Relation between primary and secondary sexual characters.

The foregoing evidence demonstrates that in hermaphrodites of *Pediculus* the state of development of the gonads, either ♂ or ♀, is independent of the development of the secondary sexual organs; moreover, that the existence or total absence of the gonads of one sex does not necessitate the presence or absence of all the other sexual organs belonging to that sex[1]. On the other hand, the development of the external and internal parts of the secondary sexual apparatus appears to be more correlated. Consequently the uterus, with its accessory glands and vagina well developed, is usually found in specimens having normal external female genitalia, and, conversely, the vesicula seminalis, with accessory glands and normal ductus ejaculatorius, coexist frequently with normal external male genitalia.

Classification of Hermaphrodites.

It is difficult to classify our material in accordance with the systems proposed by different authors whose views have been collated recently by Cockayne (1916, pp. 76–82)[2]. Nevertheless our hermaphrodites appear to conform with Dalla Torre and Friese's "Group IV. Mixed Gynandromorphism." If Cockayne's classification is followed, then our hermaphrodites comprise representatives of all three groups defined as follows by this author:

[1] This is in complete agreement with the more recent evidence regarding the relation between the primary and secondary sexual characters, especially that afforded by the experiments of Meisenheimer (quoted by Kopeĉ) and Kopeĉ (1912). These authors removed the testes and ovaries from young caterpillars of *Lymantria dispar* which nevertheless continued to develop and gave rise to normal looking moths which retained their secondary sexual characters unimpaired. Meisenheimer, and later Kopeĉ, transplanted testes or ovaries from one caterpillar to another of opposite sex, and found that the transplanted organs became connected with the sexual conduits of the opposite sex without influencing the secondary sexual characters of the imago. See Kopeĉ, S. (1912), "Untersuchungen über Kastration und Transplantation bei Schmetterlingen." *Arch. f. Entwickelungsmechanik*, xxxiii. 1–116, pls. i–v.

[2] Cockayne, E. A. (5. i. 1916), "'Gynandromorphism' and Kindred Problems." With descriptions and figures of some hitherto undescribed examples. *Journ. of Genetics*, v. 75–131, pls. xxi–xxiv, diagrams *a–k*.

"I. Genetic Hermaphrodites:

Primary sex glands of both sexes present;

II. Primary Somatic Hermaphrodites:

Sex gland or glands of one sex only, but parts of the secondary sexual apparatus, internal or external, of both sexes present;

III. Secondary Somatic Hermaphrodites:

Sex gland or glands of one sex only; secondary sexual apparatus of one sex only, that corresponds to the sex gland present. Secondary sexual characters of both sexes present...."

It is important to note that neither among the "wild" *Pediculus* or from specimens derived from crossing *capitis* and *corporis* did we discover a single specimen with the ♂ or ♀ characters localized on opposite sides of the insect's body. The non-occurrence of forms more or less approaching "halved gynandromorphs" is an indication that our hermaphrodites have much in common with those obtained by Goldschmidt and Poppelbaum[1] in Lepidoptera, these authors having obtained them by crossing *Lymantria dispar* Linn. with its variety *japonica* Motsch.

FERTILITY OF HERMAPHRODITES.

Several instances are known wherein hermaphrodites have been observed to perform sexual functions, exhibiting a normal instinct in respect to copulation besides being fertile.

Not having had an opportunity as yet of studying the behaviour of the living hermaphrodites of *Pediculus humanus*, we are unable to make a definite statement regarding their fertility; nevertheless, in view of our observations, it is possible for us to distinguish anatomically three categories of hermaphrodites in lice: those which appear to be capable of functioning (1) as males, (2) as females, and (3) that are incapable of functioning either as males or females. Among the hermaphrodites that appear capable of pairing can be distinguished sterile and fertile individuals which may serve as males or females. Moreover, among the fertile hermaphrodites which function as females, individuals occur which through some anatomical defect are incapable of expelling the fertilized eggs from their body (see p. 302). It should also be noted that hermaphrodites often possess perfectly developed testes con-

[1] Goldschmidt, R. and Poppelbaum, H. v. (1914), "Erblichkeitsstudien an Schmetterlingen II. (2) Weitere Untersuchungen über die Vererbung der sekundären Geschlechtscharaktere und des Geschlechtes." *Zeitschr. f. Indukt. Abstam. u. Vererbungslehre*, XI. 280–316, pls. i–iii. Poppelbaum, H. v. (1914), "Studien an gynandromorphen Schmetterlingsbastarden aus der Kreuzung von *Lymantria dispar* L. mit *japonica* Motsch. Mit einer Uebersicht über Ursachen und Interpretation der Gynandromorphie bei Arthropoden überhaupt." *Ibid.*, pp. 317–354, pls. iv–v. Goldschmidt, R. (XII. 1916). "Experimental Intersexuality and the Sex-problem." *American Naturalist*, L. 705–718.

taining well-formed spermatozoa, or well developed operculated eggs as already mentioned, neither the male or female elements having any means of egress from the animal's body.

Frequency of Hermaphroditism in *Pediculus humanus* and its Cause.

(a) *The percentage observed in "wild" lice and other insects.*

It is impossible to calculate the general percentage of hermaphrodites occurring among "wild" lice because of its irregular incidence. Moreover, in a large number of *corporis* bred in our laboratory during three successive years and carefully examined, we failed to find a single hermaphrodite; subsequently we came upon 6 hermaphrodites in a very short time, but still later we examined 1100 specimens of the same strain with negative results. Among "wild" lice, certain lots, composed of about 100 to 300 specimens, did not include hermaphrodites, whilst other lots (see list, p. 285) comprised many. These lots may be divided in two groups in respect to the percentage of hermaphrodites contained therein: (*a*) Lot 273 with 8·5 per cent. (85:1000), and (*b*) Lots 237, 257, 277, 278, giving a mean of 0·6 per cent. (6:1000) hermaphrodites[1]. This proportion of hermaphrodites, especially in group (*a*), is very remarkable when compared with the figures of Speyer (cited by Cockayne, *loc. cit.* p. 98) who reckons that the proportion of hermaphrodites is 1:30,000 in Lepidoptera, which, of all insects examined, have yielded the greatest number of hermaphrodites.

The presence of 19 hermaphrodites in Lot 273 of *Pediculus humanus* can only be compared with certain instances where numerous hermaphrodites were encountered in lots of Lepidoptera or Hymenoptera, instances recently classified by Cockayne (1915, pp. 95 *et seq.*) as being of a hereditary and familial nature. Whilst referring the reader to this author for further details, we may cite a case he gives (*loc. cit.* p. 97): "Mr L. W. Newman for some years bred a number of gynandromorphous *Amorpha populi*; in successive years he bred 17, 14, 11 and 2 out of totals of 2000, 1500, 1000 and 800 approximately. This year I have bred 3 from 500 of his pupae. This gives about 1 per cent. of gynandromorphs."

Furthermore, we may cite the celebrated case of Eugster's hive in Constance, to which attention was first drawn by Menzel (1862) and von Siebold (1864)[2], wherein an Italian queen bee was crossed with a German drone and yielded hundreds of hermaphrodites during three years. Of these hermaphrodites, Menzel examined 30, and von Siebold about 200, the insects showing all grades of mixture of characters pertaining to both sexes.

[1] These percentages are given roundly. The proportion of hermaphrodites is doubtless greater in such cases for we must assume that dead insects were not collected. A great mortality occurs among hermaphrodites, especially in those of ♂ type that cannot expel their eggs or suffer from the prolapse of sexual organs induced by coital traumatism.

[2] Von Siebold, C. Th. (1864), "Ueber Zwitterbienen." *Zeitschr. f. wiss. Zool.* xiv. 78–80.

(b) *The percentage of Hermaphrodites observed in crosses between* Pediculus humanus capitis *and* corporis.

The origin of the hermaphrodites observed by us in *Pediculus humanus* seems clearly indicated by the study we have made of Bacot's material. As this material is derived from the crossing of *capitis* with *corporis*, it is desirable to mention briefly the main differences which characterize these forms:

Capitis when compared with *corporis* usually appears smaller, more strongly chitinized, its antennae being relatively broader and shorter, the legs stouter, and the inter-segmental grooves at the sides of the abdomen more incised, etc. Besides these morphological differences, the insects differ somewhat in their biology, thus *capitis* is more difficult to raise experimentally and prefers to oviposit on hair. The foregoing differences fluctuate, and frequently intermediate forms are encountered in a single lot of *capitis*.

In this connection it is of fundamental importance to note that *capitis*, when raised under experimental conditions similarly to *corporis*, *i.e.* in the laboratory, after 4–5 generations changes its character and becomes similar to *corporis* both in respect to morphology and biology. This interesting phenomenon has been demonstrated by Sikora, whose observations we have confirmed (see APPENDIX I, p. 324).

Capitis and *corporis*, as already affirmed by one of us (Nuttall, 1917), may therefore be regarded as races or varieties of a single species which have become adapted to a life of parasitism mainly on the head and body respectively.

On discovering a large number of hermaphrodites in Bacot's material, we proceeded to determine their percentage in relation to the number of normal individuals, but were immediately struck by the abnormal sex-ratio. The following table includes a full enumeration of the males, females and hermaphrodites which we have made from Bacot's material, the successive generations being duly indicated:

Tabular enumeration of Bacot's material.

The material consists of 6 lots, the progeny of as many pairs or sets of parents. The first pair consisted of *corporis* ♂ and *capitis* ♀, the remainder of *capitis* ♂♂ and *corporis* ♀♀. The letters *A–S* (in brackets) relate to the list of tubes as classified and received from Mr Bacot. The signs F_1, F_2, F_3 denote the three successive generations descended from a given pair or pairs; the signs ♂̂, ♀̂ denote hermaphrodites of ♂ or ♀ character. The percentages are given roundly.

Cross I. *Corporis* ♂ + *capitis* ♀.

	♂	♀	♂̂ ♀̂
F_1 (*A*)	35	23	0
F_2 (*B*)	143	101	0
F_3 (*C*)	64	63	0
$F_1+F_2+F_3$	242 (56 %)	187 (44 %)	0 (0 %)

Cross II. *Capitis* ♂ + *corporis* ♀.

	♂	♀	☿
F_1 (*D*)	59	7	0
F_2 (*E*)	204	199	0
F_3 (*F*)	112	117	1
$F_1+F_2+F_3$	375 (53 %)	323 (46 %)	1 ($\frac{1}{7}$ %)

Cross III. *Capitis* ♂ + *corporis* ♀.

	♂	♀	☿
F_1 (*G*)	5	15	0

Cross IV. *Capitis* ♂ + *corporis* ♀.

	♂	♀	☿
F_1 (*H*)	43 (47 %)	43 (47 %)	5 (6 %)

Cross V. *Capitis* ♂ + *corporis* ♀.

	♂	♀	☿♂
F_1 (*I*)	75 (69 %)	26 (25 %)	7 (6 %)

Cross VI. *Capitis* ♂ + *corporis* ♀.

	♂	♀	☿♂	
F_1 (*J*)	128	16	0	
F_2 (*K*)	104	2	20	
F_2 (*L*)	82	17	31	—parents of (*O*) and (*P*)
F_2 (*M*)	90	28	10	—parents of (*Q*) and (*R*)
F_2 (*N*)	92	7	10	—parents of (*S*)
F_3 (*O*)	22	9	5	
F_3 (*P*)	16	31	15	
F_3 (*Q*)	100	17	13	
F_3 (*R*)	52	8	2	
F_3 (*S*)	7	32	4	

The descendants of **Cross VI** give the following totals:

	♂	♀	☿♂
F_1 (*J*)	128	16	0
F_2 (*K, L, M, N*)	368	54	71
F_3 (*O, P, Q, R, S*)	197	97	39
$F_1+F_2+F_3$	693 (71 %)	167 (17 %)	110 (12 %)

Considerations regarding Bacot's material.

Cross I, the sole one in which the ♂ was *corporis*, did not yield hermaphrodites among the 429 descendants. These, however, possess a character in common with the lots that comprise hermaphrodites in exhibiting a numerical preponderance of ♂♂ (56 per cent.). The strikingly large proportion of ♂♂ in subsequent crosses (*v. infra*) was already observed by Bacot.

Note on normal sex-ratio.

In this connection it should be recalled that normally the ♀♀ preponderate over ♂♂ (see Nuttall, *Parasitology*, x. pp. 114–117, xi. pp. 219–220). To determine the sex-ratio the mortality taking place during development should be excluded to obtain correct figures. This has only been done once (Nuttall, *loc. cit.*) where 100 out of 102 first stage larvae were raised from the egg to maturity and yielded 43 per cent. ♂♂ and 57 per cent. ♀♀.

The preponderance of ♀♀ is also shown in counts made of normal "wild" lice or such as have been raised without regard to the mortality during development. Thus in a publication by Hase (1915, p. 28), which has recently become available, this author states that among 4382 "wild" lice the different stages were present in the proportions: 100 ♂♂, 175 ♀♀ and 233 larvae; whence we reckon that the ♀♀ represented ca. 63 per cent. of the adults. Moreover, our recent examination of 2769 such normal adults shows 59 per cent. of ♀♀[1].

Cross II. This gave a numerous progeny, about 700 individuals in which the males predominated (53 per cent.), but one hermaphrodite being found. Therefore, if a larger number of individuals had been present in the case of Cross I, doubtless hermaphrodites would have been found therein.

Cross III possesses no interest because of the small number of individuals derived therefrom.

Crosses IV and **V** are interesting since they yield 6 per cent. of hermaphrodites in the first generation.

Cross VI is the most interesting because the progeny was raised through three generations and comprised a large number of individuals (970) including 110 hermaphrodites. The first generation, F_1, of this cross, although devoid of hermaphrodites, exhibits a strong numerical superiority of males over females (128:16). The F_2 generation yielded 71 hermaphrodites, their appearance being accompanied by a great increase in the proportion of males to females (368:54). The same result is visible in the F_3 generation, but the figures are somewhat less striking (197:97).

The foregoing evidence demonstrates that an abnormal sex-ratio occurs in the progeny of crosses between capitis *and* corporis, *a great diminution in the proportion of females to males is observable, this being accompanied by the appearance of a large number of hermaphrodites*[2]. The phenomenon is analogous to that observed by Goldschmidt to which we refer on p. 313.

Since a large number of hermaphrodites can be obtained by crossing *capitis* with *corporis*, it is obvious that the occasional occurrence of hermaphrodites among "wild" lice is readily understandable. Frequent oppor-

[1] These figures, based on the descendants of numerous males and females, taken collectively, are not affected by the observation of Hindle (1917, *Parasitology*, ix. 259) that certain pairs yield either ♂, ♀, or ♂♀ offspring.

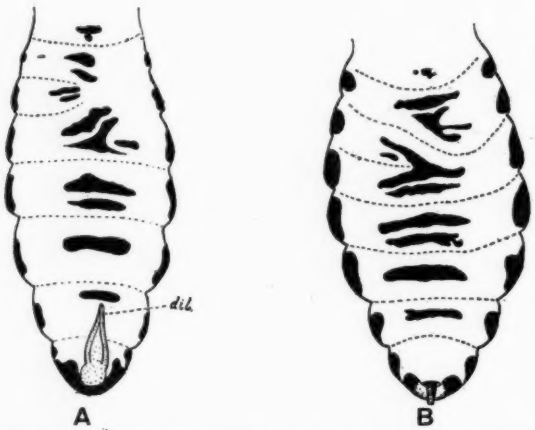
[2] The circumstance that Bacot (as he informs us) removed a very few specimens here and there from the tubes containing the material, does not affect our conclusions, for the insects removed were of the nature of "random samples," not being examined critically.

tunities arise under natural conditions for both races of lice to intermingle, as will be found by reference to APPENDIX II which follows (p. 325).

II.

SOME OTHER ABNORMALITIES IN *PEDICULUS HUMANUS*.

The abnormalities already described as occurring in hermaphrodites are (1) fragmented dorsal bands [Specimens 12, 19, 20, 22, etc.]; (2) distortion of the male or female genitalia [in numerous specimens]; (3) the presence of a supplementary gonopod [Specimen 47]; (4) double vesica penis [Specimen 83]; (5) dilator not fusing to a point but ending in two rami [Specimens 53, 83]; (6) various invaginations, etc. [numerous specimens]; (7) duplication of posterior abdominal lobes [Specimens 29, 31, etc].



Text-fig. 24. *Pediculus humanus* race *corporis*, ♂♂ (A) and (B). Lot N. 265, British, raised in Cambridge, with abnormality of dorsal bands. In (A) the dilator (*dil.*) is protruded and bent down upon the dorsal surface of the abdomen. (N. del.)

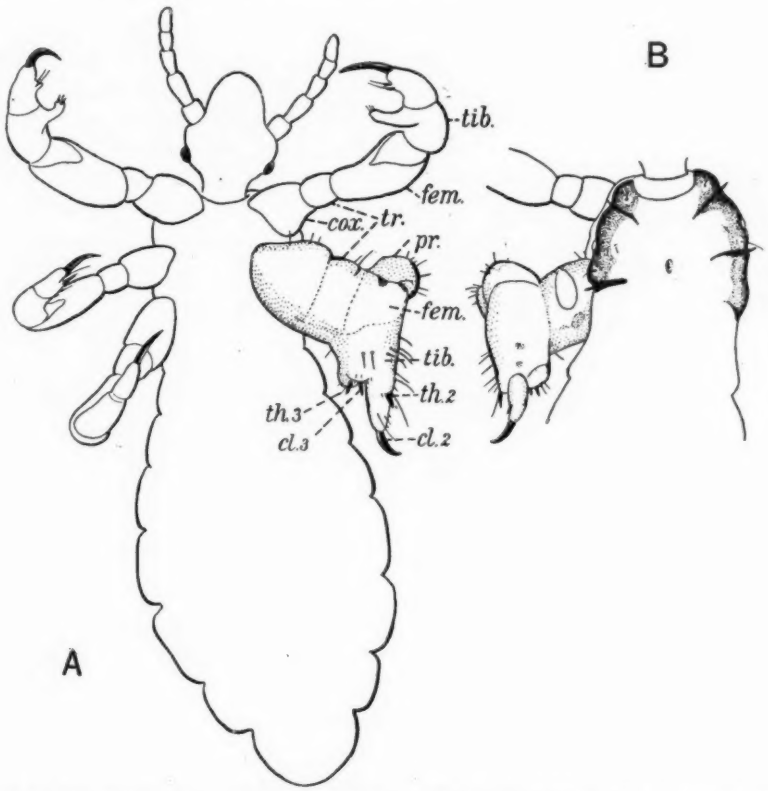
Apart from the foregoing, we have observed other abnormalities, unconnected with hermaphroditism, which possess considerable interest:

Abnormalities affecting the dorsal bands in the male.
(Text-fig. 24.)

In Lot N. 265, *P. humanus* race *corporis* of British origin, raised on black cloth in the Quick Laboratory, we found two males which presented a similar appearance in respect to the dorsal bands. In one specimen (A) the second, third and fourth pairs of bands are abnormal, the third pair appear reduced and pushed to the left by the obliquely displaced and deformed succeeding bands. The second specimen (B) differs from the foregoing as illustrated.

We have raised the progeny of both these males, crossing them with normal females, but the first generation only yielded normal specimens.

On the other hand, among hundreds of the same stock as the foregoing, are found a ♂, similarly deformed, which, on dissection, revealed three normal testes, two on one side and one on the other. The three testes contained ripe spermatozoa. All the other organs appeared normal.



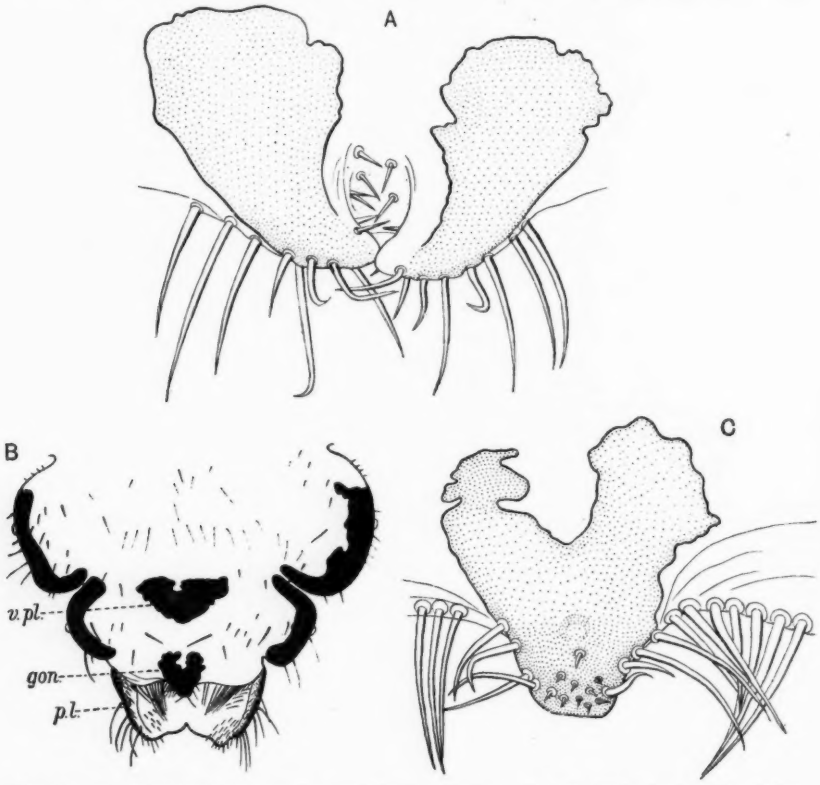
Text-fig. 25. *Pediculus humanus*, cross between *capitis* and *corporis*, ♂ (Bacot's Lot I.), showing leg abnormality. (A) Ventral aspect of whole specimen; (B) dorsal aspect in part. (N. del.)

Abnormality of the legs.

(Text-fig. 25.)

A male specimen, contained in Lot I. of Bacot, the offspring of *capitis* ♂ and *corporis* ♀ (see p. 316), presents a peculiar leg abnormality. The second and third legs of the left side are fused together to form a large mass which is curved posteriorly. Nevertheless it is possible to recognize the different parts composing the insect's leg. These parts have lost their mobility, but

faint grooves indicate the articulations. As shown in Text-fig. 25 A and B, the fused coxae (*cox.*) and trochanters (*tr.*) are well developed, the fused femurs (*fem.*) on the contrary are shortened and show an anterior protuberance (*pr.*) the significance of which is difficult to explain. The fused tibiae (*tib.*), forming an angle with the foregoing structures, are unequally developed, the



Text-fig. 26. *Pediculus humanus* race *capitis* ♀, abnormal. Lot N. 229*e*, from a Tamil boy, Federated Malay States. Illustrating abnormalities in the structure of gonopods and ventral plates as observed in four specimens: (A) gonopods closely approximated, with interspace much reduced; (B) gonopods fused in the median line; (C) gonopods fused in the median line in another specimen, more highly magnified, to show arrangement of sensory hairs. All four specimens had sub-triangular ventral plates of small size and abnormally distant from the gonopods. (N. del.)

tibia of the third leg being reduced, whereas that of the second leg bears a terminal segment and claw (*cl.* 2). This claw is curved outwardly toward its reduced thumb (*th.* 2). The tibia of the third leg terminates in a blunt rounded process bearing two spines which represent a reduced claw and thumb spine (*cl.* 3 and *th.* 3). The fusion of the legs is accompanied by a

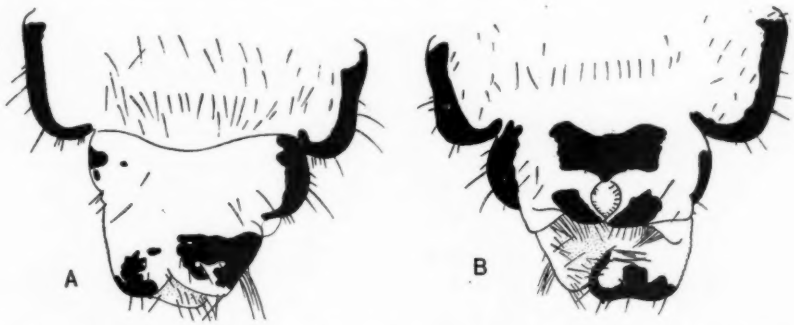
shortening and malformation of the left side of the thorax, causing a lateral curvature of the insect's body as illustrated.

Leg abnormalities in Arthropods, especially in insects, are not rare; in hitherto recorded instances they consist, however, in the duplication and not in the fusion of adjoining members as illustrated in our specimen.

Abnormalities confined to gonopods and ventral plates.

(Text-fig. 26.)

In Lot N. 229 *e*, *P. humanus* race *capitis* from a Tamil boy, Federated Malay States, were found four females with abnormal gonopods. Specimens I and II show a tendency on the part of the gonopods to fuse as illustrated at (A); the gonopods approach each other in the median line whilst the intermediate space is much reduced in size and the minute hairs are few and abnormally disposed (compare with Text-fig. 5). The ventral plate is sub-triangular and placed at a considerable distance from the fused gonopods.



Text-fig. 27. *Pediculus humanus* race *capitis* ♀, abnormal. Lot N. 260, from an East Indian boy, British Guiana. The last abdominal segment is deformed. (A) dorsal and (B) ventral aspect. (N. del.)

Specimens III and IV show the complete fusion of the gonopods in the median line. They form a single strongly chitinized process bordered with sensory hairs, some of the latter encroaching in one instance (C) upon the outer surface of the structure. A minute pit, lying centrally, appears to represent a vestige of the inter-gonopodial space.

Abnormality of posterior abdominal lobes of female.

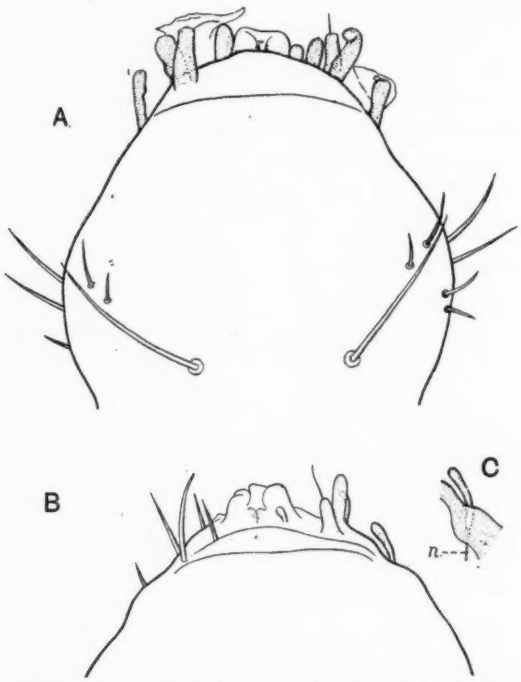
(Text-fig. 27.)

In Lot N. 260, *P. humanus* race *capitis* from an East Indian boy, British Guiana, we found a female with the last abdominal segment asymmetrical, the left posterior lobe being hypertrophied so as to overlap the opposite lobe ventrally. The chitinization of the last segment and its structure is very unequal, as illustrated.

Abnormalities of spiracles and pleural plates.

In Lot N. 280, *P. humanus* race *corporis*, from a Mkamba native, Nairobi, British East Africa, we found a darkly pigmented male with atrophied pleural plates on the first two abdominal segments of the right side and on the first segment of the left side. The spiracles connected with these plates are likewise more or less atrophied.

In Lot N. 285, *P. humanus* race *capitis*, from natives, Bogota, Central America, we found a female having the third and fourth spiracles of the right



Text-fig. 28. *Pediculus humanus*, cross between *capitis* and *corporis*, ♀♂. Specimens 120, 121. Anterior portion of head in two specimens (A) and (B). Ventral aspect, showing hypertrophied sensory hairs. (C) detail from specimen (B) showing nerve ending (*n.*). (N. del.)

side atrophied and non-functional; the pleural plate connected with the third spiracle is obsolete, that connected with the fourth is much reduced.

Abnormality in structure of peri-buccal hairs.

(Text-fig. 28.)

The anterior part of the head in *P. humanus*, as we know, bears a number of symmetrically disposed sensory hairs. Among Bacot's hermaphrodites (Specimens 120, 121) we found two examples wherein extraordinary club-

like or flattened chitinous structures occurred about the peri-buccal region. These structures are unquestionably hypertrophied hairs, for they occupy corresponding positions to such hairs, show transition forms, and communicate at their base with a terminal nerve ganglion (Text-fig. 28 c). This abnormality may have arisen prior to the last ecdysis. It is noteworthy that it was observed only in two specimens of one family.

Malformations due to accident.

As in all insects, malformed limbs may arise owing to their *premature hardening* whilst in a confined space, for instance when ecdysis is unduly prolonged. Pediculi with truncated limbs are frequently encountered, one or more legs, or an antenna being deficient. This is due to accident. Repeated and varied experiments have shown that *amputated limbs are not regenerated.*

III.

CONCLUSIONS.

I. Hermaphroditism.

The following conclusions are based on the study of a very large material, 155 hermaphrodites, which were examined in detail and yielded a complete series of forms beginning with those of male type and ending with those of female type, the co-existing characters of both sexes being present to a varying degree.

All of our hermaphrodites can be classified as belonging to Friese's "Mixed Gynandromorphs," and they include representatives of Cockayne's three groups that are described as Genetic, Primary Somatic, and Secondary Somatic Hermaphrodites.

None of our specimens accord in any way with "halved gynandromorphs," but they resemble the "intersexual" forms of Goldschmidt[1].

The state of development of the gonads in our hermaphrodites is not in accord with that of the secondary sexual organs.

Hermaphroditism in *Pediculus humanus* is often accompanied by secondary malformations, viz., fragmentation of the dorsal bands, disorientated proliferation of the genitalia of one sex, and various invaginations, devaginations and prolapses of the genitalia. These prolapses, in the male organs, are due to atrophy of the retractor muscles and basal plate, whilst in the female organs the prolapses are either due to abnormal development or coital traumatism.

The anatomical structure of our hermaphrodites indicates that they may be either sexually non-functional or functional, serving, in the latter case, as males or females in respect to copulation.

The material studied by us consists of two classes, (*a*) that obtained

[1] Reference on p. 313.

from "wild" pediculi or such as were raised by us in the laboratory, and (*b*) that obtained by crossing *capitis* and *corporis*. In "wild" pediculi the few lots which comprised hermaphrodites contained 0·2 to 8 per cent. of hermaphrodites. In the progeny of Bacot's crosses between *capitis* and *corporis*, however, some families gave over 20 per cent. of hermaphrodites.

The appearance of hermaphrodites in crosses between *capitis* and *corporis* is always accompanied by a great decrease in the proportion of females to males.

Since the hermaphrodites found among "wild" pediculi are morphologically similar to those obtained by crossing *capitis* and *corporis*, and both of these races of *Pediculus humanus* have ample opportunities for intermingling in nature as we have shown, we conclude that the hermaphrodites occasionally encountered among "wild" lice are similarly derived from crosses between *capitis* and *corporis*.

II. Other abnormalities.

Besides abnormalities connected with the genitalia of hermaphrodites, we have observed others, unconnected with hermaphroditism, affecting the structure of the dorsal bands in males, the posterior abdominal lobes in females, the spiracles and pleural plates, besides remarkable cases wherein, respectively, legs II and III were fused into an elephantine limb, the gonopods were fused in the median line, and the peribuccal hairs were extraordinarily hypertrophied.

III. *Capitis* may be converted into *corporis* in respect to its morphology.

When *capitis* are bred in boxes, they gradually acquire all the morphological characters of *corporis*. *Capitis* and *corporis* constitute but races of *Pediculus humanus*.

APPENDIX I.

Evidence proving that *capitis* may acquire all the characters of *corporis*.

We are indebted to Sikora (IX. 1917, pp. 280, 284) for being the first to discover that *capitis* may acquire the morphological characters of *corporis*. This author raised a strain of *capitis*, obtained from Warsaw, through 4–5 generations whilst confined in boxes. She records that the insects were then found to have lost all the characters of head-lice; they had attained a large size, the females averaging 4·22 mm. in length (minimum 3·96 mm., maximum 4·72 mm.), their legs being as long as in *corporis*.

Whilst Bacot found that *capitis*, after being reared in boxes in the manner he employed for *corporis*, underwent an adaptation whereby they were more easily reared under experimental conditions, he makes no mention in his publications that the insects likewise undergo an alteration in their morphology. He informs us (III. 1919), however, that he had observed an

increase in the size of the females and the number of eggs they laid, also that the insects became less active.

On 14 XI. 1917, Mr Bacot sent us some living specimens (N. 248) of *capitis* that he had bred for two years in the laboratory and, on examination by us, they were found to possess characters that were intermediate between those of typical *capitis* and *corporis* respectively.

On 22 XI. 1918, we received a further consignment (N. 287) of the same stock from Mr Bacot, his "1915 strain," which we are at present breeding; the lice are in every morphological detail like *corporis* having lost all the supposedly "specific" characters of *capitis*.

On the last-mentioned date, Mr Bacot likewise sent us (N. 288) a lot of *capitis* described as his "1915–17 strain," because, owing to an accident, his 1915 strain had become mixed with a fresh 1917 strain. The mixed strain mostly resembled typical *corporis*, a few specimens only showing intermediate characters.

We may add that Howlett (XI. 1917, p. 186) raised *capitis* upon his body and that of his Assistant in India, and that he found 75 per cent. of the F_2 generation, consisting of ca. 40 individuals, resembled *corporis* in "chitinization and colour," and that the remainder would be regarded as aberrant forms of *corporis*. Whilst chitinization and colour are not distinctive for the two races of lice, it is possible that Howlett's strain of *capitis* may also have undergone modifications in structure.

As we see from the foregoing records, *capitis* bred for two years in boxes had mostly assumed the characters of *corporis*, whilst after three years they could under no circumstances be taken for anything but a pure strain of *corporis*. Without experiments wherein such modified "*capitis*" or typical "*corporis*" are raised under normal conditions upon the head, it is impossible to say how long a period must elapse before they will assume typical *capitis* characters.

APPENDIX II.

Evidence as to the opportunities for intermingling of *capitis* and *corporis* in nature.

Capitis *on the head and* corporis *on the body of one host.* Although there is but one published record available to show how frequently man may be infested with both *capitis* and *corporis*, it proves sufficiently that he often harbours these lice simultaneously. An instance, in a woman, is cited by Nuttall (XI. 1917, p. 86), and such cases could easily be multiplied, especially if long-haired persons were chosen for examination, such individuals being much more prone to head-lice.

Hase (1915 *a*, pp. 9–11), who examined about 1000 persons in Poland during the German occupation, supplies the following record of the prevalence of head-lice and body-lice among a poor and mainly Jewish population:

	Total verminous	Infested with *capitis*	Infested with *capitis* and *corporis*
	%	%	%
Children, *i.e.* boys and girls up to 15 years	73	60	13
Women	90	55	35
Men	58	29	29

Capitis *may occur on the body* (alone). It is proved that *capitis* may occur on the body and lay nits upon the body hair; it may become established on hairy parts of the breast, in the axillae, or indeed be entirely confined to the pubic region (Nuttall, *loc. cit.* pp. 86, 94, 96). In thirteen women infested with head-lice and cursorily examined by Sikora (IX. 1917, pp. 280–282), five showed larvae and nits upon the neck and shoulders. In a mild case of pediculosis *capitis* (N. 282) recently observed by one of us (N.), there was clear evidence that the insects wandered down the back, almost to the waist, by night. We can record three instances of the capture of numerous *capitis* on shirts of East Indians, British Guiana (N. 259, 261, 262).

Capitis *occurs at times with* corporis *on the body.* Several instances of the intermingling of *capitis* and *corporis* in considerable numbers on man's body have come to our notice in specimens collected for us by trustworthy entomologists abroad: N. 258, from an East Indian, British Guiana; N. 236, from beneath a bandage on a negro carrier's leg, Nairobi, British East Africa; N. 237, from several negro patients, Nairobi (the lot comprised 2 hermaphrodites); N. 277 from a negro (Kikuyu), Nairobi (the lot comprised 2 hermaphrodites). Dr P. H. Ross, who sent the specimens from Nairobi, states that negroes invariably, when ill, sleep with their blankets pulled over their heads, a habit, we may add, which would greatly promote the intermingling of the two forms of lice, even more indeed than confinement to bed.

Whilst corporis *is rarely found on the head, it has been seen to wander up the neck to the base of the head or upon the collar* (Nuttall, *loc. cit.* pp. 83, etc.).

Corporis *has been found infesting the hairy parts of the body and it often oviposits on body hair* (though, as we know, it occurs mainly on clothing). In addition to the evidence already published by Nuttall (XI. 1917, pp. 83, 91), we would note the following: Semon and Barber (IX. 1917, p. 181) record that of 257 cases of pyodermia in soldiers, attributable to pediculosis, no less than 190 were found to have *corporis* nits upon the pubic and axillary hair when closely examined. Sikora (IX. 1917, p. 281) records having found many nits on hair that had apparently been laid by *corporis.* Stendal (1917, p. 1374) is convinced that the nits laid on man's body-hair lead to the reinfestation of soldiers that have been bathed. Smith (V. 1918, p. 519) moreover states that he confirmed the previous authors' observations, adding that it is not exceptional for *corporis* to oviposit "on pubic (and occasionally on axillary and peri-anal) hair thus defeating the anti-parasitic measures in ordinary use."

Lloyd (I. 1919, pp. 42, 85) reports an experiment wherein *corporis* adults were released upon a man's abdomen (on the skin about the umbilicus),

the man, who was kept in bed, being clothed in flannelette pyjamas; a dozen nits were laid overnight upon the pubic hair. This and the other statements of this author but confirm what Nuttall (*loc. cit.*) had already stated regarding the habits of *corporis*.

Experiments with capitis. Head-lice, when placed inside the collar, wander to the head or are lost (Sikora, *loc. cit.*); when placed on the body, after at first showing a distinct tendency to wander to the head, the offspring of such lice grow less prone to wander headwards, whilst succeeding generations of head-lice adapt themselves completely to a life of parasitism on the body (Howlett, XI. 1917, p. 186).

The foregoing evidence demonstrates that there are ample opportunities in nature for the intermingling of *capitis* and *corporis*, when they infest man, because they invade each other's feeding grounds.

REFERENCES.

See Bibliography in *Parasitology*, X. 1–42, 582–586, and to be published.

EXPLANATION OF PLATES XII—XVII.

PLATE XII.

Pediculus humanus race *capitis* ♀, dorsum. Specimen 12, well pigmented, showing fragmented dorsal bands (see text, p. 290).

PLATE XIII.

Pediculus humanus race *capitis* ♀. Specimen 12 (the same as in Pl. XII). Dorsal view of abdomen showing internal organs in cleared specimen. Two testes (*t.*) on the left side and one on the right; vesicula seminalis (*v.sem.*) and ductus ejaculatorius (*d.ej.*) obliquely placed; two large ova (*ov.*) with opercula completely formed, one surmounted by the terminal portion of an ovarian tube (see text, p. 290).

PLATE XIV.

Pediculus humanus race *corporis* ♀. Specimen 13, cleared, viewed ventrally. Showing one testis on the insect's right side (left in figure); vesicula seminalis and ductus ejaculatorius slightly pressed backward by six ova of which five are shown in the figure; a gonopodial invagination (*gon.invag.*), containing sensory hairs, is seen on the left side of the animal in the last segment (see text, p. 290).

PLATE XV.

Pediculus humanus race *corporis* ♀. Ventral aspect of the posterior part of the abdomen in three specimens:

Fig. 1. Specimen 1. ♂ ventral plate separated in two portions. Gonopods almost symmetrical. Basal plate (seen by transparency) very broad.

Fig. 2. Specimen 2. ♂ ventral plate of left side of insect fused to ♀ ventral plate. Penis protruded with dilator. Posterior abdominal lobes of ♀ very small, rudimentary. The dorsal aspect of this specimen is shown in Pl. XVII, fig. 6.

Fig. 3. Specimen 3. Showing the bipartite ventral plate of ♂. Gonopods asymmetric.

PLATE XVI.

Fig. 1. *Pediculus humanus* race *corporis* ♀. Specimen 5. ♂ ventral plate bipartite, ♀ ventral plate and gonopods rendered salient by prolapsed vagina. Dilator twisted.

Fig. 2. *Pediculus humanus* race *capitis* ♀. Specimen 12 (the same as in Pls. XII, XIII). ♂ ventral plate bipartite. ♀ ventral plate small, asymmetric. Gonopodial spot (*gon.s.*) on left side of insect.

Fig. 3. *Pediculus humanus* race *corporis* ♀. Specimen 7. ♂ ventral plate bipartite. ♀ ventral plate roughly annular. Vagina prolapsed. Two pairs of protrusions bearing sensory hairs and probably representing the posterior abdominal lobes (*x*) and gonopods (*y*) of ♀.

PLATE XVII.

Pediculus humanus race *corporis* ♀, except Fig. 8 ♂. All from Lot 273, collected in Sydney, New South Wales.

Fig. 1. Specimen 9. ♂ ventral plate bipartite, the intervening space occupied by a strongly chitinized invagination (*invag.gen.*, slightly schematized) representing the external ♀ genitalia.

Fig. 2. Specimen 14. Gonopodial invagination with sensory hairs (corresponding to *g.i.* in the following Fig. 3).

Fig. 3. Specimen 14. ♂ ventral plate and gonopodial invagination (*g.i.*) and gonopodial spot (*gon.s.*).

Fig. 4. Specimen 1. The same specimen as figured in Pl. XV, fig. 1, but seen in dorsal aspect. Posterior abdominal lobes rudimentary.

Fig. 5. Specimen 16. Structures similar to those described in Fig. 3.

Fig. 6. Specimen 2. The same specimen as that figured in Pl. XV, fig. 2, but seen in dorsal aspect. It shows posterior abdominal lobes (*p.l.*).

Fig. 7. Specimen 17. Structures similar to those shown in Figs. 2, 5.

Fig. 8. Specimen 26 (♂). Chitinous invagination with sensory hairs (*h.*) situate as shown in Text-fig. 11 (p. 294).

Fig. 9. Specimen 15. Structures similar to those shown in Figs. 2, 5, 7.

KEY TO LETTERING IN PLATES.

acc.gl. = accessory gland of ♂ genitalia; *an.* = anus; *b.p.* = basal plate of ♂ genitalia; *d.b.* = dorsal bands; *d.ej.* = ductus ejaculatorius; *dil.* = dilator (♂); *ext.* = antero-lateral extension of ventral plate in ♀; *gon.* = gonopod; *gon.invag.* and *g.i.* = gonopodial invagination (abnormal); *gon.s.* = gonopodial spot (abnormal); *h.* = hair or hairs, sensory: *invag.gen.* = invaginated genitalia (abnormal); *m.* = muscle; *mg.* = midgut; *ov.* = ova or ovary; *p.l.* = posterior abdominal lobes of ♀; *pen.* = penis; *rect.* = rectum; *t.* = testis; *tr.* = tracheae; *vag.p.* = vaginal prolapse (abnormal); *v.pl.* = ventral plate of ♂ or ♀; *v.sem.* = vesica seminalis.

THE SYSTEMATIC POSITION, SYNONYMY AND ICONOGRAPHY OF *PEDICULUS HUMANUS* AND *PHTHIRUS PUBIS*.

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I.

The lice which infest man belong to the order **Anoplura** Leach 1817, containing two sub-orders, (i) **Siphunculata** Meinert 1891 and (ii) **Mallophaga** Nitzsch 1818. The family Pediculidae Leach is included in the Siphunculata[1]. Owing to the confusion which still persists in the literature regarding the nomenclature and systematic position of the two sub-orders of Anoplura, it appears expedient to review the evidence upon which the statement contained in the preceding paragraph is based.

Linnaeus (1758, ed. x) classified "insects" chiefly in accordance with their wing structure. He divided them into seven orders, the last of which, the **Aptera,** represented a miscellaneous assemblage corresponding to what we know to-day as Apterygogenea + Suctoria + Mallophaga + Siphunculata + Isoptera + Corrodentia pp. + Arachnoidea + Crustacea + Myriopoda + Diptera pp.

Fabricius (1775, *S. Ent.*), contrary to Linnaeus, classed "insects" chiefly according to the structure of the mouthparts. He divided them into eight "classes," the last, named the **Antliata,** comprising what we know as Diptera + Siphunculata + Mallophaga + Arachnoidea pp. + Crustacea pp.

De Geer (1778, *Mém.* VII) took both the mouthparts and wing structure into account. He failed to give his groups names; these were supplied subsequently by Retzius (1783) as hereinafter indicated. The insects were divided

[1] Anoplura (ἄνοπλος, unarmed, + οὐρά, tail).
Siphunculata (siphunculus, a little tube, referring to the mouthparts).
Mallophaga (μαλλός, fleece + φαγεῖν, to eat).

into two general classes: Alata and Aptera. The **Aptera** [Retz.] contained two Orders, the second **Gressoria** [Retz.] containing the class **Aucenata** [Retz.] = Apterygogenea + Corrodentia + Siphunculata + Mallophaga nob.

Latreille (1796, p. 175) based his classification on the morphology of the mouthparts, wings, etc. His group **Parasita** = the Mallophaga + Siphunculata of to-day.

Clairville (1789, *Helvet. Ent.*) under **Pododunera** included Apterygogenea and other apterous insects.

Cuvier (1805, *Leçons*) reverted to the older method of classification according to the mouthparts. His group Aptères = Suctoria + Siphunculata + Mallophaga + Acaridae.

Lamarck (1816, *Hist. Nat.*) gives the order "Arachnides antennées trachéales," with Section 2. "Arachnides acaridiennes" (= Mallophaga + Siphunculata).

Leach (1817, *Zool. Misc.* III, p. 64) developed the conception of Swammerdam and Ray of classifying insects according to their mode of development. He divides Insecta accordingly into two classes: **Ametabolia** and **Metabolia.** The latter contains two orders, the second being the **Anoplura** (= Mallophaga + Siphunculata).

Nitzsch (1818, p. 282) founded the order **Mallophaga** but placed sucking lice under Hemiptera. Many authors have followed Nitzsch in referring sucking lice to Hemiptera (cf. Railliet, 1895, p. 823; Gerstäcker, Enderlein, *v. infra*).

Burmeister (1835–38, *Handbuch*) divides Ametabolia into two groups, (*a*) **Haustellata** which includes Pediculida and (*b*) **Mandibulata** which includes Mallophaga. (See also Denny, 1842, p. 3.)

Gerstäcker (1863, *Handbuch*) gives the order Hemiptera as comprising what we know to-day as Hemipteroidea + Siphunculata + Mallophaga.

Finally, Shipley (1904, *Zool. Anz.* XXVII, p. 261) divides the class Insecta into 22 orders; to the two orders Mallophaga and Siphunculata, he gives respectively the new names *Lipoptera* (from the Greek λιπ (λείπω)) and *Ellipoptera* (from the Greek ἐλλιπ (ἐλλείπω)). By giving new names to but seven of the 22 orders Shipley makes all the names of the orders terminate in "-ptera," which makes for uniformity in nomenclature.

We may now turn our attention to more recent authors who have given special attention to the systematic position of the Siphunculata and Mallophaga. It should be noted that many of these authors use the name Anoplura as synonymous with Siphunculata this being incorrect, for Anoplura Leach included both sucking and biting lice. Therefore, so as not to confuse the issue I shall refer throughout, as heretofore, to Siphunculata when referring to sucking lice in quoting from other authors who misapply the name Anoplura.

The old view of Nitzsch that **Siphunculata** are Hemiptera has been held by a number of authors, the view having been defended by Enderlein (1904, p. 134) who sought to homologize their mouthparts with those of Rhynchota.

Enderlein placed the Siphunculata under Rhynchota as a sub-order, degrading Siphunculata Meinert (1891), Pseudorhynchota Cholodkowsky (1903) and Lipognatha Börner (1904) to synonyms of "Anoplura" Leach. Enderlein would therefore separate Siphunculata and Mallophaga widely, this being contrary to the views of other authors both before and after his publication appeared.

Latreille (1796), Leach (1817) and Denny (1842) all agreed in placing Siphunculata and Mallophaga close together in the system, a proceeding that has been amply justified by subsequent research.

Melnikow (1869, pp. 153–186) found the Siphunculata and Mallophaga very similar in their embryology. Meinert (1891, pp. 58–83) found that the Pediculina differ from Rhynchota and Mallophaga; he therefore founded a new order, Siphunculata, to include sucking lice, these being characterized by the absence of external mouthparts like those of other insects. Meinert therefore took up an intermediate position but did not support Enderlein. Cholodkowsky (1903, pp. 120–125) agrees fully with Melnikow, and brings Pediculidae and Mallophaga together in a new order **Pseudorhynchota,** a thankless proceeding since this name necessarily falls into synonymy. Handlirsch (1903, p. 730) also reached the independent conclusion that Pediculidae and Mallophaga are closely allied, he places Corrodentia, Mallophaga (Nitzsch) Handl., and Siphunculata Meinert in three successive orders in the sub-class **Blattaeformia** (see also Handlirsch (1906–8), *Handb.* p. 1290), regarding the Siphunculata (which include Pediculidae) as Mallophaga that have adapted themselves to blood-sucking. Handlirsch (1905, pp. 664–670) disagrees entirely with Enderlein; to Handlirsch the mouthparts of Pediculidae appear more primitive than those of Hemiptera, they seem to be directly derived from a chewing type, and in searching for such a type he always came back to Mallophaga; Enderlein's own observations actually confirm Handlirsch in his view that Pediculidae are derived from Mallophaga.

Börner (1904, p. 527) does not agree with Cholodkowsky in associating Pediculidae and Mallophaga together under Pseudorhynchota, and degrades the latter to a synonym of Siphunculata Meinert; Börner, because of the difference in the mouthparts, places Mallophaga in a sub-section of the **Acercaria** and the Siphunculata in the new sub-section **Lipognatha** Börner (1904). Fulmek (1907), Mjöberg (1910) and Harrison (1915) likewise agree that the Siphunculata and Mallophaga are closely allied. Gross (1906, p. 347) rightly remarks that altogether too much attention has been rivetted upon mouthparts and their homologies to the exclusion of everything else; he draws attention to the very close resemblance he found in the structure of the ovaries in two species of Pediculidae and two species of Mallophaga when compared in this respect. Of the two super-families of Mallophaga, the Ischnocera and Amblycera, Harrison (1916, pp. 218–221) finds that the Ischnocera are distinctly more affiliated to the Siphunculata, as indicated by the structure of the antennae, legs, thorax, the digestive and tracheal systems, the position

of the heart and fat body, and the structure of the reproductive organs, all of which differ from what is seen in Rhynchota. Mjöberg (1910) has moreover noted the resemblance between the eggs of Siphunculata and Mallophaga in respect to all essential details, including the micropyle apparatus and the "Eistigma" at the base. This accumulated evidence should finally dispose of Enderlein's contention.

As previously stated, many authors continue to use the name Anoplura in place of Siphunculata. This is done by some of the writers above quoted and others (Sharp, 1899, p. 599; Shipley, *Zool. Anz.*, 1904, p. 261; Silvestri, 1910, p. 198; Patton and Cragg, 1913, p. 527; Castellani and Chalmers, 1913, p. 631; Cummings, 1912–1916, in various papers; Ferris, 1916, p. 129; Grimshaw, 1917, p. 13, etc.). *Since, however, the name Anoplura Leach* (1817) *was applied to both Siphunculata and Mallophaga, and in this sense agrees with modern views, it should henceforth be used in its original sense only, there being no justification for continuing to apply it to Siphunculata alone.*

It is evident from the foregoing statements that the following, remodelled, systematic definitions are called for so as to obviate confusion in the future:

II.

ORDER ANOPLURA Leach 1817[1].

Characters of Order: wingless insects which undergo incomplete metamorphosis and live continuously as ectoparasites on warm-blooded animals upon whose feathers or hair (or clothes in man) they cement their eggs. Antennae typically 5-articled, when 3- or 4-articled they show derivation from 5-articled type. Eyes reduced or absent. No ocelli. Mouthparts reduced. Legs modified for clinging. Thoracic segments more or less fused. Abdomen of adult composed of nine apparent segments. Functional spiracles: typically seven pairs, one thoracic and six abdominal.

The Anoplura are divided into two sub-orders: (1) Mallophaga and (2) Siphunculata which, but for the structure of the mouthparts and subsidiary differences, have many characters in common.

Sub-order I. Mallophaga Nitzsch 1818.

Characters of Sub-order: Anoplura with mandibulate mouthparts, feeding only on feathers or hair and the epidermal detritus of their host (exceptionally on extravasated blood). They chew their food. Thorax divided, meso- and metathorax usually fused. Eyes always present. Antennae 4- or 5-articled. Thoracic stigmata ventral. Tarsi with one or two claws.

The Mallophaga are mostly parasites of birds, relatively few (Trichodectidae, Boopidae) occur on mammals.

[1] Mr L. Harrison has kindly aided me in drafting the three definitions relating to the characters of Anoplura and the sub-orders Mallophaga and Siphunculata.

SUB-ORDER II. SIPHUNCULATA Meinert 1891.

CHARACTERS OF SUB-ORDER: Anoplura with haustellate mouthparts, feeding only on blood which they suck after piercing the skin of the host. Piercing apparatus, when at rest, retracted within a diverticulum opening into the floor of the pharynx anteriorly. Thorax undivided (except in *Haematomyzus*). Eyes present or absent. Antennae 3-, 4-, or 5-articled. Thoracic stigmata dorsal. Tarsi with one claw. Parasites of mammals.

The Siphunculata are divided into four families:

	Salient differential characters
1. Pediculidae Leach 1817. Type genus: *Pediculus* Linnaeus 1758	With eyes, head not retracted into thorax, antennae 3–5-articled.
2. Haematopinidae Enderlein 1904. Type genus: *Haematopinus* Leach 1817	Eyes absent or very rudimentary, head retracted into thorax.
3. Echinophthiriidae Enderlein 1904. Type genus: *Echinophthirus* Giebel 1871	Antennae 4–5-articled, parasitic on marine animals only.
4. Haematomyzidae Enderlein 1904. Type genus: *Haematomyzus* Piaget 1869	With prothorax distinct, head prolonged anteriorly as a long narrow tube, tarsi with a flattened hair-like structure terminating in a hook and arising alongside the claw, no tibial thumb[1].

N.B. This classification of the Siphunculata is the one usually accepted. The group was at first known by very few species, and it is only within relatively recent years that more have been defined. A multiplicity of genera have been founded, some obviously on characters of doubtful value, *i.e.* slight differences in external structure. The classification of the group as a whole will have to be recast when more species are known, their relations established, and their essential anatomical structures have been adequately studied. Such studies will require the use of other methods than the usual one of treating specimens with caustic potash and mounting them in balsam.

We are only concerned herein with Pediculidae:

FAMILY I. PEDICULIDAE LEACH 1817, p. 64.

CHARACTERS OF FAMILY: Siphunculata with head not prolonged anteriorly like a tube. Chitinous piercing organs, when retracted, barely attaining the thorax. Eyes large, protuberant, clearly pigmented. Antennae 3–5-articled. Tibia with thumb-like process and single incurved claw; no triangular pretarsal sclerite between tibia and tarsus (in contrast to Haematopinidae). Parasites of Primates.

The Pediculidae contain two sub-families: (1) Pediculinae, and (2) Pedicininae:

[1] The mouthparts, on cursory examination, appear aberrant. They require to be studied so as to render the systematic position of the family secure.

SUB-FAMILY I. PEDICULINAE Enderlein 1904, p. 136.

CHARACTERS OF SUB-FAMILY: Antennae 5-articled in all stages except first stage larvae where there are but three distinct articles.

The Pediculinae contain two genera: (1) *Pediculus*, (2) *Phthirus*:

Genus I. Pediculus Linnaeus 1758, p. 610.

CHARACTERS OF GENUS: Body elongate. Abdomen moderately elongate, segmentation distinct. Head constricted proximally in a neck-like manner. Legs strong, all fairly uniform in size in all stages, but leg-pair I of ♂ stouter and with larger thumb than pairs II–III; leg-pair III of ♀ with blunt baso-ventral femoral spur, pairs I–II normal. Gonopods in ♀ consisting of two dorso-ventrally flattened and convergent hooks, concave internally and serving to encircle and grasp a hair during oviposition. Hosts: man, and occasionally monkeys and apes that have been in contact with man[1].

The genus contains but one species: *Pediculus humanus* Linn., having three races: *capitis*, *corporis* (*v. infra*), and *schäffi*.

Genus II. Phthirus Leach 1815, p. 77.

CHARACTERS OF GENUS: Body cordiform. Abdomen very short, broad, segments crowded together, the three penultimate segments bearing lateral processes increasing in size backward. Legs similar in both sexes, pair I small and slender with long fine claw, pairs II–III very thick with short, stout claws ending in knobs. Hosts: man, twice recorded on dog.

The genus contains one species: *Pthirus pubis* (Linn.) Leach (*v. infra*).

SUB-FAMILY II. PEDICININAE Enderlein 1904, p. 136.

MAIN CHARACTER OF SUB-FAMILY: antennae with three distinct articles in adults. Hosts: monkeys and apes.

The sub-family contains two genera:

1. *Pedicinus* Gervais 1844, III, p. 301.
2. *Phthirpedicinus* Fahrenholz 1912, p. 22.

III.

PEDICULUS HUMANUS LINNAEUS 1758.

SYNONYMY.

1671. *Pediculus ordinarius* Redi 1671, Pl. XVIII, brief mention in text.

1747. *Pediculus humanus* Linnaeus 1747, *Fauna Suecica* (ed. I), p. 337, sp. 1153.

1758. *Pediculus humanus* Linnaeus 1758, *Systema Naturae* (ed. X), p. 610: "Habitat in capite et vestimentis hominis."

1761. *Pediculus humanus* Linnaeus 1761, *Fauna Suecica* (ed. altera), p. 475, sp. 1939: "Habitat in homine, praesertim in capite Puerorum, & vestimentis Nautarum, Militum, etc. Maximos in Fodinae Fahlunensis cryptis calidioribus reperi. Qui in vestimentis victitat ab eo, qui in capite vivit, non differt ut species, sed tantum varietas."

[1] Animals in menageries or in confinement.

1767. *Pediculus humanus* Linnaeus 1767, *Systema Naturae* (ed. XII, Reformata), II. p. 1016, head-lice and body-lice regarded as varieties numbered 1 and 2 respectively: "Habitat in capite et vestimentis hominis:—Varietas Capitis durior, coloratior; Vestimentorum laxior, magis cinerea."

"Problema qui solvat, cur aliae ejusdem speciei familiae mordicus Capiti inhaerunt, aliae corporis vestimentis, is facile plurium morborum contagiosorum naturam intelligat." Which Barbut (1781, p. 329) translates: "He that could solve the problem why some families of the same species stick to the head, others to the clothes, would easily understand the nature of many contagious diseases."

1775. *Pediculus humanus* Linn. in Fabricius (1775, p. 804): "Habitat in capite et vestimentis humanis. In pueris gulosis frequentissimus."...."Varietas capitis durior, coloratior, vestimentorum laxior, magis cinerea." He gives a brief and useless description.

1778. *Pediculus humanus capitis* de Geer 1778, *Mém. Hist. Ins.*, VII. pt 1, fig. 6. Head-louse.

Pediculus humanus corporis de Geer 1778, *Ibid.* fig. 7. Body-louse. "Il y a donc une différence palpable entre ces deux sortes de poux, et qui semble indiquer qu'ils sont d'espèce différente, à moins qu'on ne veuille plûtôt, comme a fait M. de Linné, les regarder comme deux variétés. Quoiqu'il en soit, on pourroit les distinguer par les dénominations suivantes: (1) *Pediculus* (*humanus capitis*) cinereus, thorace abdomineque fascia interrupta nigra marginatis; (2) *Pediculus* (*humanus corporis*) albidus totus immaculatus."

1783. *Pediculus humanus* Linn., *a. capitis, β. corporis* de Geer. Retzius (1783): de Geer, *Gen. et Spec. Ins.* p. 201, sp. 1323 *α–β*.

1803. *Pediculus humanus* Linn. in Latreille (1803), *Dict. Hist. Nat.*, XVIII. p. 403; 1804, p. 93, sp. 1: "le pou du corps"; a definite restriction of the name to the body-louse.

Pediculus cervicalis Latreille 1803, *Dict. Hist. Nat.*, XVIII. p. 403; 1804, p. 94, sp. 2. He makes a distinct species of "le pou de tête."

Note: If this were a good species, the name *P. capitis* (de Geer 1778) would have priority, first having been applied to the head-louse as a possible variety of *P. humanus*, mark the bracket which is often omitted by those who regard *capitis* as a valid species.

1810. *Pediculus humanus* Leach 1810, p. 77, *fide* Stephens (1829).
Pediculus cervicalis Leach 1810, *Ibid.*

1817. *Pediculus humanus* Leach 1817, p. 66, sp. 1. Syn. "*Ped. pubescens a* Olfers 80, body louse or Tailor's louse."

Pediculus cervicalis Leach 1817, p. 66, sp. 2. "*Ped. humanus* var. Linn. *Syst. Nat.*, I. 1016."

1818. *Pediculus capitis* Nitzsch 1818, III. p. 305.

Pediculus vestimenti Nitzsch 1818, *Ibid.* Name commonly applied by German authors (*vide* Eysell, 1913, p. 48, etc.), and those who follow them. The name has no validity (= *P. h.* race *corporis*).

1824. *Pediculus tabescentium* Alt 1824 (= *P. h.* race *corporis*). Cited as a valid species by Goldfusz and Burmeister, Denny, etc., but rightly condemned by Landois, and by Piaget (1880, p. 625, q.v.); not mentioned by Dalla Torre (1908, p. 8).

1829. *Pediculus humanus* Stephens 1829, p. 329, sp. 9318: "Body-louse, or Tailor's louse." This author gives references to Berkenhout, Shaw, Turton, Samouelle and Langley (see bibliogr.) and "Stew. II. 278," and gives "*Pe. capitis* de Geer (teste Nitzsch)" as a synonym.

Pediculus cervicalis Stephens 1829, p. 329, sp. 9319: "Head-louse." This author gives an inaccessible reference to Samouelle (see bibliogr.) and records "*Pe. vestimenti* de Geer (teste Nitzsch)" as a synonym.

1842. *Pediculus capitis* Denny 1842, p. 13, Pl. XXVI, fig. 2.
Pediculus vestimenti Denny 1842, p. 16, Pl. XXVI, fig. 1.

1874. *Pediculus capitis* Giebel 1874, p. 30, Pl. I, fig. 1–2.
Pediculus vestimenti Giebel 1874, p. 27, Pl. I, fig. 5.

1880. *Pediculus capitis* Piaget 1880, p. 619, Pl. L, fig. 2.
Pediculus vestimenti Piaget 1880, p. 623, Pl. L, fig. 3.
Pediculus consobrinus Piaget 1880, p. 626, Pl. LI, fig. 4 (= *P. h.* race *capitis*). From *Ateles paniscus* (*pentadactylus*). Given as a valid species by Dalla Torre (1908, p. 8). Piaget himself was more cautious, for he put "n.sp. (?)" after the name. He founded the supposed new species on the size of the head, form of thorax, and finer details, the head being "quite rounded in front," although otherwise it was much like *capitis*. An examination of Piaget's figures and text proves that he was merely dealing with a short and broad strain of *capitis*. Neumann (1910, p. 410) also refers Piaget's doubtful species to *capitis*.

1908. "*Pediculus capitis* de Geer" in Dalla Torre (1908, p. 8), includes "*P. humanus* Csiki 1904, *Rovart Lapok*, II. 180," as a synonym.
"*Pediculus corporis* de Geer" of many authors has no status. It is given as a valid name by Dalla Torre (1908, p. 8); Castellani and Chalmers (1913, p. 631), etc.

1910. *Pediculus affinis* Mjöberg 1910, pp. 169, 258, Pl. V, fig. 8 (photo.) and text-figs. 85, 151 (♀, ? shrivelled); specimens taken from *Ateles* sp. I agree with Cummings (III. 1916, p. 255) that there is nothing in Mjöberg's description or figures to indicate that he was dealing with other than *P. h.* race *capitis*. I have moreover examined typical dark specimens of *capitis* (♀ and larvae), at the British Museum, that had been taken from *Ateles paniscus* at the Zoological Soc. Gardens, London, these being the same specimens referred to by Cummings (*loc. cit.*) as corresponding to "*affinis*." Cummings dismisses "*affinis*" as "probably a straggler from human beings, establishing itself on *Ateles*." It is possible, however, that Cebidae harbour *capitis*-like lice naturally. These lice are small, have the 5th spiracle-bearing abdominal segment more prominent than is usual in *capitis* (♀ and larva), whilst the ♂ has the thumb of the first tarsus reduced. I would add the following records of this strain of *capitis* from further hosts. N. 301, ♀ and larvae from *Cebus hypoleucus* and N. 299, ♂♂ and larvae from *Ateles geoffroyi*, gifts of Hon. N. C. Rothschild; ♂ and larvae and part of ♀ from *Ateles ater*, in Denny's collection at Oxford. It remains to be determined if Cebidae in a wild state harbour such lice.

1910. *Pediculus schäffi* Fahrenholz 1910, p. 57, Pl. III, figs. 2, 6 and text-fig. 1 (eggs), specimens taken from a recently imported *Simia troglodytes* (chimpanzee) at the Zoological Gardens, Hanover. The heavily infested animal had been treated for lice of which a few ♀♀ and larvae were received for examination. Judging from the author's figures and measurements he must have indeed examined very few specimens. The only indications he gives that may point to a new species are, (*a*) the presence of a blunt spur basally on coxa II in ♀ and larva, (*b*) the very prominent lateral protrusion of the last abdominal segments in a ♀, (*c*) the more tapering basal end of the egg; his further "specific" characters may be dismissed as without significance. Fahrenholz concludes that the larva moults soon after hatching because in a mounted specimen of a larva, which he assumes had just issued from the egg, a well chitinized 2nd stage larva is seen within the 1st larval

skin. (In my opinion the author was probably dealing with a shrivelled specimen that was about to moult and remained clinging accidentally to an empty egg shell.) We have recently encountered this louse in the Denny collection at Oxford and shall refer to it again in a future paper. On the evidence at hand, *P. schäffi* must be regarded provisionally as a race of *P. humanus*.

1912. *Pediculus capitis* Fahrenholz 1912, p. 2, Pl. III, figs. 3, 4, text-figs. 1, 3, 7.
Pediculus corporis Fahrenholz 1912, p. 2, Pl. III, figs. 1, 2, text-fig. 2.

1913. ? *Pediculus lobatus* Fahrenholz 1913, *Zool. Anz.*, XLI. p. 373, taken from *Ateles pan* (*vellerosus*). No description; probably = race *capitis*.

1913. ? *Pediculus oblongus* Fahrenholz 1913, *Zool. Anz.*, XLI. p. 373, taken from *Hylobates concolor* (*mülleri*) and *Symphalangus* (*Hylobates*) *syndactylus*; probably = race *capitis*.

1913. *Pediculus humanus* Linn., according to Castellani and Chalmers (1913, p. 631), includes: "*P. capitis* de Geer 1778, and *P. cervicalis* Latreille 1803."

1916. *Pediculus mjöbergi* Ferris 1916, p. 136 = *P. affinis* Mjöberg (*v. supra*) renamed, because this name is preoccupied, *i.e.* *P. affinis* Burmeister 1839 (*Gen. Rhyn.* No. 10) representing another species.

? 1917. *Pediculus capitis* var. *maculatus* Fahrenholz, from negroes.
Pediculus capitis var. *angustus* Fahrenholz, from Japanese.
Pediculus corporis var. *marginatus* Fahrenholz, from Japanese.

The foregoing three supposed varieties are mentioned by Sikora (1917, p. 172) as having been recently published by Fahrenholz. Although the latter author's paper is inaccessible to me, I venture to assert that these names will not stand and that they must fall into the synonymy of *P. humanus*. Their author apparently fails to appreciate the variability of the species from having access to limited material.

1917–19. *Pediculus humanus* Linnaeus 1758, in Nuttall (II. 1917, p. 294), includes *capitis* and *corporis* although they show biological differences; Nuttall (XI. 1917, p. 83), regards *capitis* and *corporis* as at most racial forms of *P. humanus*. Keilin and Nuttall (1919, pp. 279 et seq.), record the occurrence of hermaphrodites in crosses between *capitis* and *corporis*, this supporting the view that head- and body-lice constitute races; nevertheless *capitis* bred for four to five or more generations in captivity assumes all the morphological characters of *corporis*.

VULGAR NAMES: O. Eng. *lus*, Eng. *louse*, Du. *luis*, Ger. *Laus* (Kopflaus, Kleiderlaus), Dan. and Swed. *lus*, Fr. *pou*, It. *pidocchio*, Span. *piojo*, Portug. *piolho*, Russ. *vosh*, Lat. *pediculus*, Gr. *φθείρ*.

ICONOGRAPHY OF *P. humanus*.

In the following list of references to publications illustrating the species *P. humanus*, only those are cited that possess either special historical interest or contribute useful information. The illustrations, dealing with lice, that are to be found in the literature are as a rule astonishingly bad. References to publications containing illustrative matter are indicated by the letter I in the Bibliography.

1634. MOFFETT, p. 259, a crude woodcut of a louse.

1665. HOOKE, Pl. XXXV, ventral aspect of ♀, the figure ca. 40 cm. long; very good, shows the gonopods, etc. This figure is reproduced in smaller size by Albin (1736), Pl. XLII.

1668. Redi, Pl. XVIII, pidocchio ordinario (*corporis* ♀); also Redi (1671), Pl. XVIII, *Pediculus ordinarius*; interesting early figures.

— Leeuwenhoek, ed. 1807, Pl. XVI, figs. 1–8, figures the head, mouthparts, "sting" of ♂, claws, empty nits attached to threads of wool.

— Swammerdam, ed. 1682, Pl. VII, illustrates the nit before and after hatching, a larva, and apparently a ♀ (*corporis*); the 1758 edition has Pls. I and II showing mouthparts, gut, ♀ genitalia, nervous system. Remarkably good, much better than the figures of many recent authors.

1778. deGeer, Pl. I, figs. 6–10, ♀♀, ♂, copulatory apparatus, leg I, head (*capitis* and *corporis*).

1781. Barbut, Pl. XVIII (*corporis*), a very poor figure compared to that of Hooke, the tarsi figured with two claws that grasp like pincers.

1811. Ramdohr, Pl. XXV, fig. 4 (*corporis*), gut, fairly good illustration.

1829–44. Guérin-Meneville, Pl. II, coloured figs. 5, 6, comparing *corporis* and *capitis*, no text. He demonstrated the essential differences since pointed out by many authors, some of whom, even within the last two years, supposed that they were contributing something new.

1855. Leuckart, Pl. VII, figs. 1, 2, the egg and its micropyle apparatus.

1861. Murray, text-figs. 1–3 and 2 plates, mainly illustrating claw structure in lice from different parts of the world.

1864. Schjödte, 2 text-figs., mouthparts protruded.

1865 *a*. Landois, Pls. II–IV (*corporis*), egg, anatomy, genitalia, muscles (also in *capitis*).

1865 *b*. Landois, Pl. XXXVIII (*capitis*), mouthparts, spiracle, etc.

1869. Melnikow, Pls. VIII–XI (*capitis*), figs. 22, 23, 30, 31, 37–39, embryology.

1880. Piaget, Pl. L, figs. 2, 3 (*capitis, corporis*); Pl. LI, fig. 4 ("*consobrinus*"); see note to Piaget in Bibliography regarding older authors who illustrate lice.

1890. Blanchard, figs. 672–679, inaccurate, show the mouthparts in different stages of protrusion, etc. (*capitis*).

1891. Meinert, Pl. I, mouthparts.

1893. Cholodkowsky, figs. 1–6 (*capitis*), egg and embryo.

1904. Enderlein, fig. 2 (*corporis*), mouthparts; also 1905, figs. 1–5, mouthparts.

1906. Gross, Pl. XXI (*capitis*), ovaries and egg.

1906. Pawlowsky, figs. 1–13 (*corporis*), mouthparts; also 1907, Pls. II–VI, figs. 1–33 (*capitis* and *corporis*), sexual organs.

1908. Dalla Torre, figs. 1 *a*, 1 *b* (*capitis*), general structure.

1910. Fahrenholz, Pls. and text-figs. (*capitis* and "*schäffi*"); also 1912, Pl. and text-figs 3–7 (*capitis, corporis*, and "*schäffi*"), chaetotaxy, etc.

1913. Patton and Cragg, Pl. LXVI, figs. 5, 6; Pl. LXVII, figs. 1–5; Pl. LXIX, figs. 1–5; Pl. LXX, figs. 1–6; Pl. LXXI, figs. 1–7; illustrating the adult's head, external anatomy of 1st and 2nd stage larvae, ♀, egg, internal anatomy, mouthparts, sexual organs, etc. (*capitis* and *corporis*); all the figures are original and for the most part good.

1913. Martin, figs. 16–17 (*Pediculus*), longitudinal section of body showing disposition of internal organs; mouthparts, much schematized.

1913. Castellani and Chalmers, figs. 267–270 (*capitis* and *corporis* according to the legends but all evidently drawn from shrunken specimens of *capitis*-type as evidenced by short palps and stout legs); drawings by Terzi showing ♂♂ and ♀♀ in dorsal aspect, being the first figures which show the femoral spur on leg III of ♀.

1914. NEUMANN and MAYER, Pl. XLIV, figs. 20, 21 (*humanus* ♀), good.

1915. WULKER, 1 text-fig. (*humanus*), progressive stages of development of the embryo in the egg, good.

1915. HASE, 47 figs. (*capitis* and *corporis*) mostly crude; good photographs showing immediate effects of bites in producing wheals.

1916. HARRISON, Pl. VII, 7 text-figs. (*corporis*), mouthparts.

1916. PEACOCK, text-figs. 1–8 (*corporis*), schematic, anatomy, also 1918, Pl. VI. 6 text-figs. (*corporis*), mouthparts; taken in conjunction with Harrison's, these are the best figures hitherto published.

IV. 1916. SIKORA, 3 Pl. (2 coloured) and 24 text-figs. (*corporis*), important; also IX. 1917, 3 text-figs., *capitis* and *corporis* compared.

1917. NUTTALL, Pls. III, IV, and 12 text-figs. (*corporis*), copulation and copulatory organs; also 1918, Pls. I–III, and 12 text-figs. (*corporis*), biology and morphology; also II. 1919, Pl. X (*corporis*), showing pigmentation when raised on black background in contrast to white; also Keilin and Nuttall, Pls. XII–XVIII, text-figs. 1–28 (*capitis*, *corporis* and crosses between the two), normal, abnormal, and hermaphroditic specimens; their external and internal anatomy.

1919. LLOYD, figs. 1, 3, 5 (*corporis*), ♀ in dorsal aspect (poor), internal anatomy (diagrammatic), eggs.

CONSIDERATIONS RELATING TO THE FOREGOING SYNONYMY.

1. *Valid and invalid names.*

The name *Pediculus humanus* was applied by Linnaeus (1758) to both head-lice and body-lice. He subsequently regarded head- and body-lice as two varieties of *P. humanus*, numbering them 1 and 2. Whilst de Geer (1778) inclined to the view that head-lice and body-lice were distinct species, or possibly varieties, he expressed no definite opinion either way, but suggested the names *Pediculus humanus capitis* and *Pediculus humanus corporis* whereby to distinguish the two forms.

Latreille (1803) raised the two varieties of Linnaeus to specific rank, restricted the name *Pediculus humanus* to body-lice, and gave the name *Pediculus cervicalis* to head-lice. Therefore, if body-lice and head-lice constituted distinct species, their names would be respectively *P. humanus* and *P. capitis*, *corporis* falling into the synonymy of the former and *cervicalis* into that of the latter in accordance with the rule of priority. If on the other hand body-lice and head-lice are not regarded as two species but merely as varieties or races of one species, we are justified by the rules of zoological nomenclature in reviving the binomial of de Geer whilst more clearly defining its significance, a matter he left in doubt.

In view of all the evidence at hand, which will be considered presently, I conclude, as already stated in my earlier papers, that *P. humanus* stands as a species and that it includes two races to which de Geer's names *capitis* and *corporis* should be applied. It is in this sense that these names are employed hereinafter by me.

The names *P. tabescentium* Alt 1824, and *P. vestimenti* Nitzsch 1818,

are invalid for reasons of priority (= *corporis* as defined by me). The names *maculatus*, *angustus*, and *marginatus* applied by Fahrenholz to supposed varieties of *capitis* and *corporis* (themselves but races, or varieties if liberally interpreted!), cannot be recognized, for they are surely based on faulty observation.

The specific names applied to lice (other than Pedicinidae) found on monkeys and apes, *i.e. consobrinus* Piaget 1880, *affinis* Mjöberg 1910, *schäffi* Fahrenholz 1910, *lobatus* and *oblongus* Fahrenholz 1913, *mjöbergi* Ferris 1916 (= *affinis* Mjöberg, *v. supra*), apply either to invalid or to very doubtful species and are attributed here to *P. humanus* race *capitis* which have established themselves on these animals during confinement, having been in contact with man. Until these purported species have been adequately differentiated from those occurring on man, they certainly cannot be accepted as valid. There is nothing strange about it that man's lice should occasionally establish themselves on other Primates than man. (Note that Noeller (1916) is stated to have raised *P. humanus* on the pig. See also my two records showing that *Phthirus* may parasitize the dog!)

2. *The relationship between* capitis *and* corporis.

In considering the relationship existing between these two forms which some have regarded as species and others not, it is necessary to dwell upon the supposed differences which have been considered sufficient to separate the forms specifically.

(*a*) *Morphological differences.*

Morphological differences between *typical* examples of *capitis* and *corporis* were already indicated by Guérin-Meneville (1829–44, Pl. II) by illustrations showing *capitis* with *palps* short and broad, *abdomen* having angular segments and deep intersegmental indentations laterally[1], *pigmentation* dark. In *corporis* on the other hand, the palps appear longer and slenderer, the abdominal segments are rounded with shallower intersegmental indentations, whilst pigmentation is absent. These differences have been pointed out by many subsequent writers, some indeed appear to have believed that they discovered them.

Size. Stress has been laid upon the smaller size of *capitis*. It has been asserted that the largest *capitis* is always smaller than the smallest *corporis*, even by such recent authors as Fahrenholz (1912) and Cummings (1915). That *capitis* may however exceed *corporis* in size has been pointed out by Neumann (1910), Popoff (1916) and Sikora (IX. 1917) whose statements I can confirm. Whilst *capitis* is usually smaller than *corporis*, there is no difficulty—given a sufficient number of specimens—in obtaining a series wherein in point of size the one form merges into the other.

Details of structure. According to various recent authors, *capitis* (compared

[1] Especially in adults.

to *corporis*) has (i) the *head* shorter and blunter; (ii) the *thorax* broader anteriorly (Neumann, 1910); (iii) the *legs* shorter and stouter; (iv) the *gonopods* blunter; (v) the *chaetotaxy* different; (vi) the *egg* smaller (Fahrenholz, 1912, and others). Of these differences, that exhibited in the legs generally holds for *typical* head-lice, but none of the others are constant, as I have firmly convinced myself after examining a large material. Otherwise typical *capitis* may possess gonopods as pointed as in *corporis* and *vice versa*. Whilst Fahrenholz states that the chaetotaxy in *corporis* is characterized by fewer and smaller hairs upon the ventral surface of the abdomen (he illustrates this by comparative figures), the examination of his figures, or of actual specimens, proves that the hairs merely appear fewer in *corporis* because its body surface is larger (stretched) and the hairs consequently further apart. In justice to this author, his remark should be cited that he was "much disappointed" not to find a greater difference in the chaetotaxy. Fahrenholz ignores the statements of (i) Enderlein (1905) that he could find no difference in the chaetotaxy although he considered the two forms distinct species, and (ii) Neumann (1910) that the chaetotaxy is variable, which I contest if the statement applies to the number of hairs in this situation, where the number is fairly constant, though the hairs certainly vary in length both in *capitis* and *corporis*. The point made by Sikora (IX. 1917) that the *thumb* differs in the two forms, does not stand critical examination. In typical *capitis*, derived especially from African negroes, I find the *chitinization* most pronounced, this rendering the insects tougher, but intermediate degrees of chitinization occur leading down to the thinner exoskeleton of *corporis*. According to Landois (1865*a*, p. 494) the *ventral abdominal muscles* differ in female *capitis* and *corporis*; this requires investigation.

False statements. Piaget (1880, p. 619) asserted that *capitis* differs from *corporis* in having (i) no thoracic spiracles, (ii) seven abdominal segments and five pairs of abdominal spiracles, instead of eight and six respectively. These false statements, based on inaccurate observation, would need no comment but that one or the other have been cited in all innocence by Fahrenholz (1912) and Alessandrini (1916) in support of their contention that *capitis* and *corporis* constitute distinct species.

Differences inconstant. All of the differences that earlier writers sought to establish between *capitis* and *corporis*, were dismissed as inconstant by Schjödte (1864) and Neumann (1910), except perhaps the deeper incisions between the abdominal segments in *capitis*. This difference I find cannot be relied on for it is likewise inconstant. Therefore, whilst there is no difficulty in referring a *typical* form either to *capitis* or *corporis*, there remains no constant morphological difference between the two for they are linked together by all shades of intermediate forms passing through almost imperceptible gradations in size, general shape and details of structure. *Pigmentation*, being entirely dependent on the colour of the background (*vide* Nuttall, II. 1919, pp. 206–219), does not constitute a difference.

Contradiction in the literature. The critical presentation of the foregoing evidence appears called for because of the continually recurring misstatements in text-books and the contradictions in the writings of various authors. Of recent writers, we find Cholodkowsky (1904), Enderlein (1905), Fahrenholz (1912), Hase (1915), Heymann (1915), Cummings (1915), and Alessandrini (1916) contending that *capitis* and *corporis* are two distinct species, whilst Meinert (1891) more correctly regards them as at most varieties, and Neumann (1910) ranks them as sub-species.

Evidence of raising experiments. The foregoing statements, which I base on the examination of a very large material collected from man, may perhaps appear insufficient to those in whom the belief has become rooted that *capitis* and *corporis* represent two species. There is however a final piece of evidence, *i.e.* typical *capitis* lose all their distinctive morphological characters when raised experimentally on man under conditions which are favourable for the propagation of *corporis*, and they acquire all the morphological characters of *corporis* after four or more generations (*vide* my paper with Dr Keilin, this vol.).

The conclusion reached on the basis of morphological data above enumerated, is that *typical* capitis *and* corporis *represent the extremes in the variation of the one species* Pediculus humanus, *and that they are identical in all essential points of structure*[1].

(*b*) *Biological differences.*

Having found that morphological differences afford no support for the contention that *capitis* and *corporis* constitute two species, we may now consider the biological differences which characterize typical specimens of both forms.

Habitat on the host. It has been repeatedly asserted that *capitis* occurs only on the head and *corporis* only upon the clothing, this being regarded as a sign of the forms being two species. Even assuming that such a biological difference existed, it could not be regarded as specific. A closer examination of this supposed biological difference shows, however, that it is inconstant. Recent evidence (see Nuttall, XI. 1917, p. 86; Keilin & Nuttall, 1919, this vol.) proves that *capitis* does occur on man's body and that it lays its eggs upon his body-hair, even occasionally upon his clothing in the vicinity of the head. The assertion that *corporis* only oviposits on man's clothing has been disproved, it having been found to lay on his body-hair (*loc. cit.*), therefore it is practically certain that *corporis* is capable of occasionally ovipositing on the hair of the head. Whilst there is no denying that the one form shows a preference for the head and the other for the body, the foregoing evidence proves at any rate that their habitats are inconstant and that their areas of distribution overlap to no inconsiderable degree.

[1] These are the grounds for my statement made in an earlier paper (II. 1917, p. 294, footnote) and which was contested by some entomologists who were not aware of the evidence on which I based it.

Activity. That typical *capitis* are more active in their movements at a lower temperature than are *corporis* is well established, this depending, I believe, upon the temperature conditions prevailing in their usual habitat, that in the hair being usually lower than that adjacent to the clothed human body to which *corporis* has, within limits, adapted itself. This difference may be regarded as merely due to adaptation.

Climbing on hair. Owing to typical *capitis* being stouter limbed and usually smaller than *corporis*, they climb more rapidly along hair (Nuttall, XI. 1917, pp. 101–3), their muscles being relatively more powerful and their weight less. In this respect, *corporis* may be regarded as somewhat modified, owing to the altered surroundings in which they live, *i.e.* mainly in clothing to which they can cling with greater ease than hair. This is compensated for, however, by the habit *corporis* has acquired of gorging, which allows it to tide over fasting periods brought about by the host periodically discarding his clothing.

Feeding. There is practically no difference in the feeding habits of *capitis* and *corporis* when they have unlimited opportunities of sucking blood, for under such conditions they imbibe small meals at frequent intervals (*ibid.* p. 173). The opportunities of snatching small meals upon the head are much greater than upon the body, because the hair to which head-lice cling is rooted in the skin, whereas the clothing to which *corporis* chiefly cling (owing to insufficiency of hair upon the human body), shifts about when the body is in movement. A consequence of this is that *corporis* becomes ravenous and imbibes large meals, *i.e.* gorges at intervals determined by the resting periods of the host or the periods when he removes and replaces his clothing. This habit of gorging is one which *capitis* may, however, likewise acquire if trained to feed at longer intervals of time. It is due in my opinion to altered feeding conditions that *capitis* appears more difficult to raise experimentally than *corporis*, it must first acquire the ability to gorge.

Bearing of feeding habits on size and form. The smaller average size of *capitis* is attributed by Sikora (IX. 1917, p. 282) to the effect of its feeding ground on the insects' nutrition and possibly to a difference in the temperature of the habitat.

On the contrary, it appears to me that *capitis* should be regarded as the normal standard for comparison in seeking to explain the usually larger size of *corporis*, there being no reason to suppose that *capitis* suffers from malnutrition. By raising *capitis* under similar experimental conditions to *corporis*, that is, by altering its usual feeding habits, it becomes habituated to feeding at longer intervals and acquires with time the size and form of *corporis*. It appears to me that the periodic gorging, which necessarily leads to increased internal pressure, explains the larger size of *corporis*, in that the chitinous exoskeleton, prior to ecdysis and whilst still soft, is more stretched than is normally the case with *capitis*. It is only exceptional with *corporis* to gorge when provided with unlimited opportunities of feeding, they behave in other words like typical *capitis*. It is without doubt due to this that *corporis* raised

by me in a felt cell on the arm, where they could feed at will (Nuttall, XI. 1917, pp. 105, 161), were decidedly smaller than others raised in boxes and fed twice daily to repletion. These insects were also proportionately narrower across the abdomen as compared to those that were fed but twice daily. I am convinced that by modifying the method of feeding so as to lengthen the intervals between meals as rapidly as practicable, that *capitis* will be made to assume the form of *corporis* in a shorter time than four to five generations as observed by Sikora. Greatly increased internal pressure, consequent upon the habit of gorging, although induced periodically, would appear to me to explain the larger average size of *corporis*, particularly the stretching of the thinner portions of the integument, especially the increase in the size of the abdomen coupled with the loss of angularity in the abdominal segments and the more widely separated hairs upon the abdominal surface.

The effect of darkness no doubt is responsible for *corporis* possessing longer and slimmer antennae and legs than *capitis*. The latter is more exposed to light upon the head than is *corporis* beneath the clothing in most instances. It is of course well known that arthropods inhabiting dark places have longer antennae and legs than those living exposed to light.

Minor biological differences have been pointed out by different authors, thus the *fertility* of *capitis* is somewhat less under experimental conditions (see Nuttall, XI. 1917, p. 141), but such experiments do not afford a just measure of what takes place in nature. With time, as Mr A. Bacot informs me (III. 1919), *capitis* lay more eggs when raised in successive generations experimentally.

Copulation. The observation of Bacot (II. 1917, pp. 253, 256) that ♂ *corporis*, when paired with ♀ *capitis*, cause an undue mortality among the latter, is explained, in my opinion, by coital traumatism, due to large males copulating with small females and rupturing them. The statement of Bacot (*loc. cit.*) that *oviposition* differs in *corporis* in that these prefer to lay on cloth and lay awkwardly on hair, was not confirmed by me (*loc. cit.* p. 143), although *capitis* has been found both by Bacot and me to prefer laying on hair. This difference is however only one of degree.

Interbreeding. When *capitis* and *corporis* pair, they yield a progeny that are fertile to the third generation, as was first demonstrated by Bacot (*loc. cit.*), and there is no reason to suppose that this fertility may not continue longer.

The occurrence of hermaphrodites in crosses between *capitis* and *corporis* (see Keilin and Nuttall, this vol.) indicates that the two forms are races belonging to one species.

That corporis *is descended from* capitis *in nature* has been assumed by systematists like Mjöberg (1910, p. 169), Fahrenholz (1910, p. 65), and Cummings (1916), who regarded the two forms as separate species. Without holding the latter view, and prior to reading these authors' papers, it also occurred to me, as it has to others, that *capitis* must represent the primitive form. According to this view, primitive man was hairy all over, as his body grew naked he adopted clothing and his very ancient pedicular ectoparasites

adapted themselves to the altered conditions, finding in the fur or cloth-fibres constituting the clothing a substitute for the hair that was vanishing from the host's body surface.

Now, however, in view of the success that has been attained in modifying *capitis* in a short time so that it becomes indistinguishable from *corporis*, both structurally and biologically, I can but conclude that *P. humanus* is a species possessing considerable powers of adaptation, that the primitive form *capitis*, being in a labile state, can rapidly adapt itself to altered conditions beneath the clothing of man. Whilst in Sikora's experiments, the change of character was effected in four to five generations, a longer period was required to produce the change in Bacot's strains which we have studied. It is conceivable therefore that some races of *capitis* are more labile than others, but it is also likely that the change will be more rapidly effected by a graded process of feeding suited to bring about the rapid acquisition of the habit of gorging. There is little doubt in my mind that *capitis* is being converted into *corporis* to-day in nature, and that the latter, when man has become hairless, will constitute a species whose birth we are witnessing.

CONCLUSION.

In view of the morphological and biological evidence contained in the foregoing statement, incorporating all the information available up to the present, and reviewing the evidence critically in a manner that has not been done hitherto, I conclude that *capitis* and *corporis* merely represent two *unstable races* of one species[1], *Pediculus humanus* Linnaeus, and that they should in future be designated as follows, partly from practical considerations:

Pediculus humanus race *capitis*.
Pediculus humanus race *corporis*.

IV.

PHTHIRUS PUBIS (LINNAEUS 1758), LEACH 1815.

SYNONYMY.

1634. *Pediculus ferus* Moffett 1634, p. 200; Ray, 1710, p. 8, who writes: "Numerosè propagatur inter piles inguinum, praecipuè immundorum," they occur in the axillae, are hard to pull away, for they cling like Ricinus, and "raro item vaguntur."; Olfers, 1816, p. 83.

1671. *Pediculus inguinalis* Redi 1671, Pl. XIX.

— "*Pediculus morpio* Merr. pin. 202," cited by Linnaeus, 1761, p. 475.

[1] In my opinion, the two forms are insufficiently fixed to be regarded as varieties. In this connection it appears appropriate to quote the following passages from Poulton's *Essays on Evolution* (1908): Darwin, writing to Asa Gray in 1856, states it as his opinion "that species are only strongly marked varieties." In a letter to Hooker, Darwin wrote in 1864, "The power to remain for a good long time constant I look at as the essence of species, combined with an appreciable amount of difference." Coulton (*loc. cit.* p. 76) writes that if two forms are widely different and still syngamic (interbreeding freely) they are to be regarded as one species (witness the various races of dogs, etc.).

1747. *Pediculus pubis* Linnaeus 1747, No. 1154.

1758. *Pediculus pubis* Linnaeus 1758, p. 611; also 1761, p. 475, No. 1940: "Habitat in hominum immundorum pube et ciliis"; also 1767, p. 1017: "Hospitatur in hominis immundi pube, rarius in superciliis; pellitur Oleo Tabaci." See also Fabricius, 1775, p. 805, and 1794, IV. p. 418, who gives a brief Latin description.

1759. *Pediculus inguinalis* Reichard 1759, *fide* Eysell, 1913, p. 48, and Castellani and Chalmers, 1913, p. 631.

1804. *Pediculus pubis* Latreille 1804, p. 96, he gives a brief description; Stephens, 1829, p. 329, cites Berkenhout, and Turton (see Bibliography) and "Stew. II. 279."

1815. *Pthirus inguinalis* Leach 1815, *Ed. Encycl.* vol. IX. p. 77 (Stephen, 1829, gives the date 1810, but Enderlein, 1904, corrects it to 1915); Leach, 1814–1817, *Zool. Misc.* vol. III. p. 65, writes: "Habitat in hominis pube, grandebulis, villis, superciliis, ciliis, mustacibusque, cuti adhaerens."

1835. *Phthirius inguinalis* Burmeister 1836, *Handb. Ent.* II. pt. 1, pp. 52, 58 (*fide* Dalla Torre, 1908, p. 9); in Denny, 1842, pp. 8–11; in Giebel, 1874, pp. 23–27, Pl. I, fig. 8; in Piaget, 1880, p. 628.

1855. *Phthirius pubis* Küchenmeister 1855, p. 445.

Remarks: The specific name *pubis* Linnaeus 1758 stands, the generic name *Pediculus* is superseded by *Phthirus* Leach 1815, therefore the correct name is *Phthirus pubis* (Linnaeus 1758) Leach 1815. Note the bracket.

There is some excuse for Redi's specific name *inguinalis* persisting, but the Linnaean name must stand in accordance with the rules of zoological nomenclature.

Enderlein (1904, p. 136), Dalla Torre (1908, p. 9), and Ferris (1916, p. 138) give the name rightly as *Phthirus pubis*. The name *Phthirus* was misspelt by Burmeister (1835) and consequently by many authors since who followed in his track, spelling it *Phthirius*. The name is also frequently misspelt *Phtirius*, *vide*; Dubreuilh and Beille (1895, p. 107); Mégnin (1906, p. 87); Mjöberg (1910, p. 171); Silvestri (1911, p. 200), etc.

VULGAR NAMES: Eng. *crab-louse*; Fr. *morpion*; Ital. *piattola*; Ger. *Schamlaus, Filzlaus*; Dan.-Swed. *Flatlus*.

ICONOGRAPHY.

1668. REDI, Pl. XIX, early figure, of historical interest.
1671. REDI, Pl. XIX, the same as the above.
1829–44. GUÉRIN-MENEVILLE, Pl. II., fig. 7 (no text).
1855. LEUCKART, Pl. VII, fig. 2, egg.
1864 *a*. LANDOIS, Pls. I–V, anatomy from dissections, important.
1865 *b*. LANDOIS, Pl. XXXVIII, muscular system.
1872. GRABER, Pl. XI, figs. 1–14, mouthparts, gut, genitalia, egg.
1880. PIAGET, Pl. II, fig. 5, bad.
1904. ENDERLEIN, figs. 10, 11, head and abdominal segments.
1913. CASTELLANI and CHALMERS, fig. 271, adult, fairly good.
1913. PATTON and CRAGG, Pl. LXVI, fig. 1, ♀ in dorsal aspect.
1918. NUTTALL, figs. 1–12, morphology and biology.
1919. LLOYD, figs. 12, 13, dorsal aspect, leg III, poor.

REFERENCES.

These will be found appended to my papers quoted in the text.

FURTHER OBSERVATIONS ON THE HABITS AND PARASITES OF COMMON FLIES.

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(With Plates XVIII, XIX, 23 Text-figures and 2 Charts.)

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THE INFLUENCE OF WEATHER ON FLIES.

In the year 1915 the flies caught in traps baited with various materials and placed in different situations were recorded, and charts constructed showing the effects of various meteorological conditions on flies. "These charts showed that the curve for flies caught in traps corresponded most closely to the curve for the maximum temperature recorded by a thermometer exposed to the sun" (1916, 497 and Chart 5). During the years 1916 and 1917 traps baited daily with human excrement were exposed in sunny situations, and the flies caught in them recorded. Records of the hours of bright sunshine, of the rainfall, the velocity of the wind, the maximum temperatures indicated by thermometers exposed to the sun and in the screen, the minimum temperatures in the screen and on the grass were kept. From these observations it was possible to compare the effects of meteorological conditions on flies in three consecutive seasons.

Chart 1 shows the mean daily temperatures recorded by a thermometer exposed in the sun and the mean daily number of flies caught in a trap exposed in the open and baited with human excrement in each week during the seasons

of 1915, 1916 and 1917[1]. The three seasons were very different in character. In 1915 June, August and September were the finest months; in 1916 the early part of the season was dull, July and the early part of August very fine and the remainder of the season wet and unsettled; in 1917 April was very cold, May and the early part of June very fine and the remainder of the season wet and stormy.

A short summary of the weather conditions in each month is given in Table I.

Table I. *Showing the weather conditions during the fly seasons of* 1915, 1916 *and* 1917.

	1915	1916	1917
March	Very cold, last few days warmer	Cold, windy and wet; rain fell on 23 days	Very cold and windy; snow fell till end of month
April	Cold and windy, last few days fine	Cold and windy till 21st; later fine, warm, no rain	Frequent snow showers up to 12th; after 20th finer, but cold. "Coldest April for over half a century"
May	Bright and dry, but cold winds frequent	Up to 16th dull and damp, after 16th very fine and warm	Very fine and warm. "Warmest May for over half a century"
June	Very fine month	"Coldest June recorded at Greenwich"	Up to 17th very fine and warm; later cloudy and frequent showers
July	Unsettled, many cloudy days; rain fell on 16 days	To 6th fine and warm; 7–25 dull, windy, frequent showers; 26–31 very hot and fine	Very strong wind almost every day; several oppressive days with thunder
August	Mostly very fine	To 13th very fine and hot; afterwards windy, rainy, unsettled	"Peculiar in the exceptional violence and duration of its gales"
September	Dull and windy early; later hot and oppressive; end cold	To 20th rainy and dull; later fine	Fine on the whole; 13 days of dull weather or heavy rain
October	Cold and stormy, few good days	Very unsettled and rainy throughout	Early part wet; later fine
November	Very cold	To 8th rain and wind; later bright but cold	Fine, but very windy towards end

It will be seen by reference to Chart 1 that in 1915 flies were most abundant in August and September, in 1916 in July and the early part of August and in 1917 in May and June. In each year the curve recording the number of flies caught corresponds with the curve for the maximum temperature recorded in the sun. It is evident that the appearance of flies early in the season does not necessarily indicate a great abundance in the latter part of the season.

[1] These figures were obtained by adding together the maximum temperatures recorded daily and the numbers of the flies caught daily in each week and dividing the results by seven.

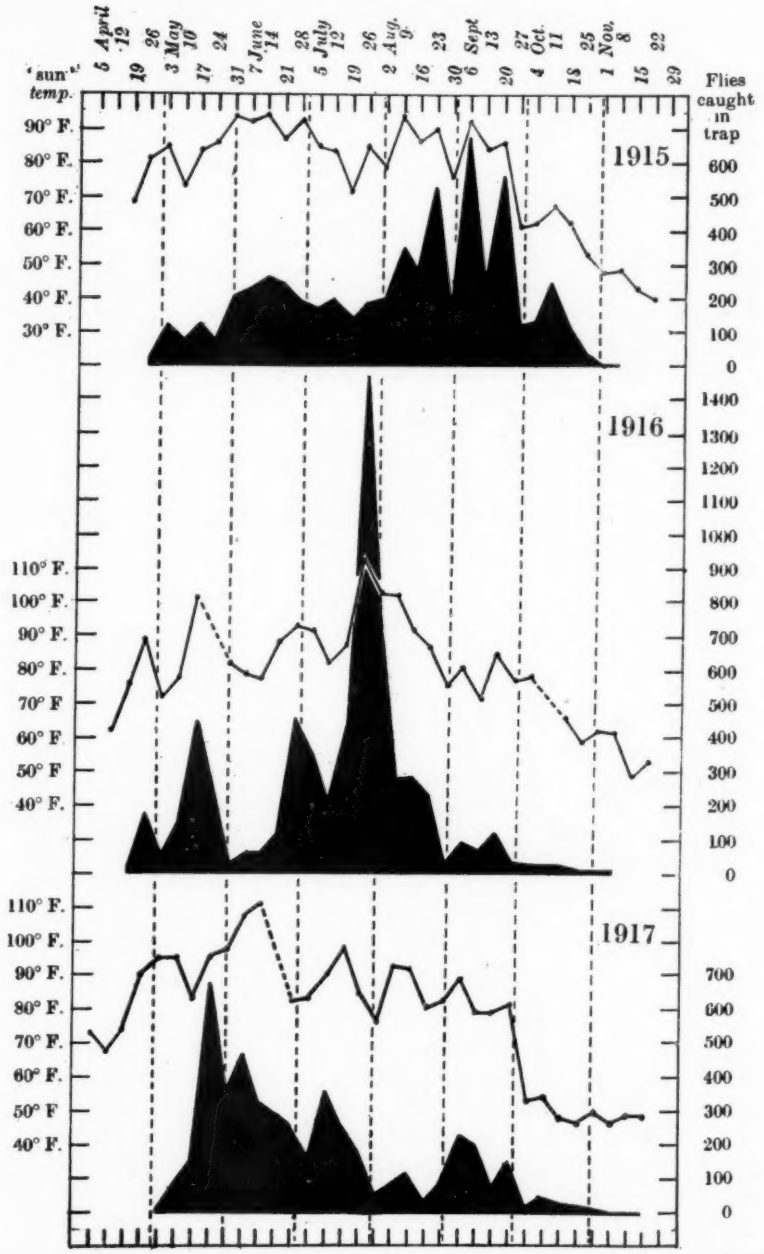

Chart 1. Weekly records of flies caught in traps baited with excrement and of "sun" temperature in the years 1915, 1916, 1917.

On several occasions the flies caught in a trap baited with excrement were counted hourly, and the maximum temperature recorded by a thermometer exposed in the sun during each hour noted. The results obtained on two consecutive days, July 26 and 27, 1916, are shown in Chart 2. On July 26 the sun first appeared at 1.30 p.m. and the afternoon was very fine. The fly curve corresponds closely with the curve for the maximum "sun" temperature. The following day was very fine and hot throughout, and the flies were most numerous about midday. This seems to be the normal condition on very fine, sunny quiet days.

The following flies were common in 1914, uncommon in 1915 and again common in 1916: *M. hortorum, G. maculata, P. albolineata, P. eriophthalma. P. greenlandica* was very common in 1916.

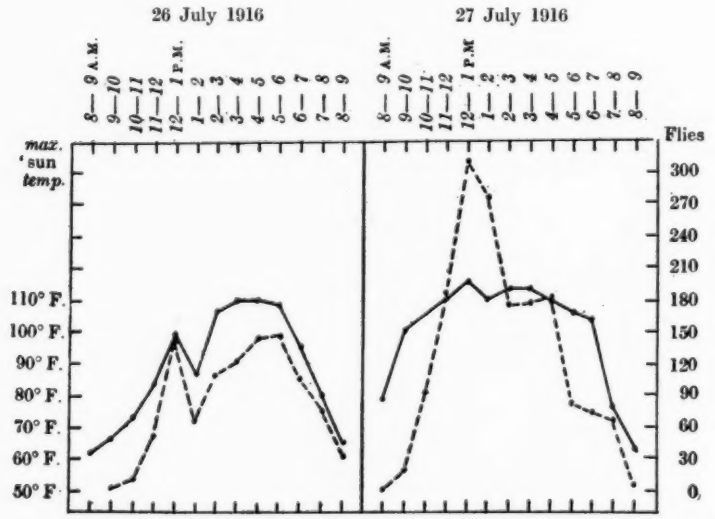

Chart 2. Number of flies caught in a trap baited with excrement (broken line) and maximum temperature recorded by a thermometer in the sun (line) during each hour on July 26 and 27, 1916.

HABITS OF FLIES. CLEANSING.

The cleansing habits of flies, especially of *S. carnaria*, were carefully studied in a large cage, 12 × 8 × 7 ft, out of doors—under conditions resembling as closely as possible those in which these flies live.

Throughout the day flies spend a very large proportion of their time, probably several hours daily, in cleaning themselves; not infrequently a leg or wing is being cleaned even in the act of feeding. Cleansing is almost invariably undertaken after feeding, and the procedures usually follow each other in a definite order. The wings are first treated on both surfaces, and they receive more attention than any other structure; next the posterior legs;

after these the anterior legs; then the middle and anterior legs; next the middle and posterior legs; finally the head and proboscis. Not infrequently the wings receive further attention at intervals between the cleansing of the various pairs of legs.

The following procedures are adopted for cleaning the wings. In cleaning the upper surface of the wing the posterior leg of the same side is brought forward and bent over the proximal part of the wing as it lies horizontally along the dorsum of the fly (Pl. XVIII, figs. 7, 8), and the leg is then drawn slowly backwards along the wing towards its distal extremity. When the leg has travelled about half the length of the wing, which in consequence has been bent downwards, the opposite posterior leg is brought across under the abdomen and placed under the wing so that the tip of the wing is clasped between the two legs (Pl. XVIII, fig. 9). As the legs pass backwards the tip of the wing is drawn between them, and when it escapes from their embrace springs back into its usual position (Pl. XVIII, fig. 11).

Sometimes the two posterior legs are used simultaneously for cleaning the upper surfaces of both wings (Pl. XVIII, figs. 10, 12, 21, 24). Each leg is brought forwards and bent over the proximal part of the wing of the same side and then drawn very slowly backwards along the wing to its distal extremity. The under surfaces of the two wings are generally cleaned simultaneously. The wings are raised and the posterior legs are brought forward and bent in such a manner that the distal part of the leg passes under the wing with the extremity of the tarsus beyond the inner margin of the wing. The wings then seem to be pressed upwards till they are almost vertical by the elevation of the legs. While in this position they vibrate with such rapidity that it is impossible to follow the movements exactly (Pl. XVIII, fig. 23).

During these procedures the fly stands on the anterior and middle pairs of legs, the latter pair assuming the position normally occupied by the posterior pair.

When the anterior pair of legs is about to be cleaned the middle pair is brought forward in order to obtain a steady position, and the fly sits erect. Then the anterior legs are thrust forwards horizontally below the head, which seems to be held higher than usual. The cleaning movements are often slow and pauses are not infrequent while the legs are applied to each other. Sometimes the tarsi appear to be crossed and rubbed together, but more frequently the pulvillus of one leg is applied to the surface of the opposite limb, and drawn slowly along it (Pl. XVIII, figs. 1, 2, 3, 13).

When the posterior pair of legs is about to be cleaned the middle pair assumes the position usually occupied by the posterior pair, the head is depressed between the anterior legs and the abdomen elevated, so that the fly appears to be standing on its head. Then the posterior legs are thrust out backwards horizontally below the abdomen and rubbed together in the same manner as the anterior legs (Pl. XVIII, figs. 5, 6, 15, 16).

The middle legs are cleaned with the aid of the anterior or the posterior

pairs of legs, and the procedure is usually rapid. When the anterior pair of legs is employed for this purpose the fly balances itself on the posterior pair and the opposite middle leg with its body tilted so as to slightly raise the side on which the operation is about to take place. Then the middle leg is brought forward, and rubbed between the anterior legs (Pl. XVIII, figs. 4, 17, 18). When the posterior pair is used the fly balances itself on the anterior pair and opposite middle leg with the abdomen raised and the middle leg is rubbed between the posterior legs (Pl. XVIII, fig. 19). A single anterior or posterior leg is never employed in cleaning a middle leg.

The abdomen is cleaned by passing one or other of the posterior legs over its dorsal surface from its proximal to its distal end.

The dorsal surface of the thorax is cleaned together with the upper surface of the wing, the movement of the leg commencing near the head of the fly.

When the head is about to be cleansed the middle legs are thrust forwards, and the anterior legs applied to the sides of the head in such a manner that

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DESCRIPTION OF PLATE XVIII.

Photographs, natural size, of male *S. carnaria* cleaning themselves out-of-doors. Exposure $\frac{1}{300}$ sec.

Figs. 1, 2, 3. Some of the positions assumed when the anterior legs are being rubbed together. The middle pair of legs are directed forward in order to maintain a steady position.

Fig. 4. The two anterior and the left middle legs are being rubbed together, while the body is balanced on the other three legs.

Figs. 5, 6. Positions assumed when the posterior legs are being rubbed together. The middle legs are now directed backwards.

Figs. 7–12. Some of the positions assumed when the wings are being cleaned. In all cases the middle legs are directed backwards. Fig. 7. The right posterior leg resting on the proximal part of the right wing, while the left posterior leg is being elevated preparatory to being applied to the upper surface of the left wing. Fig. 8. The left posterior leg passing down the upper surface of the left wing; the right posterior tarsus is under the tip of the left wing. Fig. 9. The distal part of the right wing clasped between the two posterior legs as they are drawn backwards. The wing has been so bent that upper surface is directed outwards. Fig. 10. The posterior legs passing over the upper surfaces of the wings. Fig. 11. Left wing about to escape from the embrace of the posterior legs. Fig. 12. Wings bent and applied to the sides of the abdomen by the pressure of the posterior legs.

Fig. 13. The anterior legs being rubbed together. Middle legs directed forwards. Side view.

Fig. 14. The proboscis being cleaned with the aid of the anterior legs. Middle legs directed forwards. Side view.

Figs. 15 and 16. The posterior legs being rubbed together. Middle legs directed backwards. side view.

Figs. 17 and 18. Anterior pair and right middle leg being rubbed together. Side view.

Fig. 19. Posterior pair and right middle leg being rubbed together.

Fig. 20. Head being cleaned between the anterior legs.

Fig. 21. Right wing elevated by right posterior leg beneath it; left wing depressed by left posterior leg passing over it.

Fig. 22. Both wings depressed by the posterior legs passing over them.

Fig. 23. Both wings elevated by the posterior legs beneath them.

Fig. 24. Posterior legs raised before application to the wings.

Figs. 13–24. The flies are resting on the edge of a piece of plate glass.

the head is bent downwards bringing its posterior surface into view. The legs are then moved rapidly upwards and downwards causing the head to jerk from side to side. So rapid are the movements that the head appears to be rotating (Pl. XVIII, fig. 20).

The proboscis is cleaned with the anterior pair of legs, and the movements may be rapid or very slow. Both legs are used simultaneously, and the pulvilli, applied on each side of the extended proboscis, are passed along it from its proximal to its distal extremity. During this procedure the fly sits erect (Pl. XVIII, fig. 14).

The males of *S. carnaria* were chosen as subjects for these observations, because they are large, not readily disturbed, are somewhat sluggish in their motions, and have very large pulvilli, which are easily observed. Similar procedures for cleaning themselves are adopted by most of the commoner species of flies, and also by the hymenoptera parasitic on them.

During the seasons of 1916 and 1917 the habits of the two closely allied species, *C. erythrocephala* and *C. vomitoria*, were carefully noted. *C. erythrocephala* was caught in traps almost daily, but *C. vomitoria* only occurred commonly in the traps on fine days with little wind. *C. vomitoria* and *H. dentipes* seem to dislike great heat and are seldom found on windy days, especially if very hot. On the other hand *Lucilia* and *O. leucostoma* are seldom caught in traps on sunless days, but are very common and active on hot, sunny days.

It was noticed in both years that newly emerged flies are greatly attracted to excrement, and that in the early part of the season decomposing animal matter attracts few flies, presumably because the majority are not ready to oviposit.

In October 1917 some much decomposed animal remains containing many small larvae were buried to a depth of 18 inches. This material was exhumed on February 13, 1918, when the larvae were found to be alive and nearly full fed.

It may be of interest to record the fact that when digging in the face of a sand pit on April 20, 1917, two male *Onesia cognata* were found at a depth of 18 inches from the surface, and some inches from the face of the pit. A distance of 9 feet separated the two flies, which were very sluggish, but soon became active on exposure to the sun.

EMPUSA DISEASE.

The writer has shown previously (1916, p. 507) that records relating to the infection of flies, other than house-flies, with empusa are rare. He described the infection in four specimens of *H. dentipes*, two of *F. canicularis* and in *C. erythrocephala*.

In the year 1916 very careful observations were made and 34 specimens of *H. dentipes* infected with the disease were found outside between July 5 and September 11. In that year it was first seen in *M. domestica* on September 27.

In 1917 and 1918 infected specimens of *H. dentipes* were found in July and the disease was first noticed in *M. domestica* on September 13, 1917, and on July 25, 1918. In *H. dentipes* the symptoms develop with very great rapidity. For example an apparently normal specimen caught in the morning was dead and showed well marked rings round the abdomen by 6.30 in the evening. After a certain period a halo of spores is thrown out round the body. As previously suggested (1916, p. 507) the infection may spread from such flies as *H. dentipes*, which develop the disease in the middle of summer, to *M. domestica* or its larvae.

In 1916 infected specimens of *Lucilia* were found outside on July 7 and August 22 (Pl. XIX, fig. 4) and in 1917 a specimen on July 2.

In 1917 six infected specimens of *F. canicularis* were found indoors on October 1 and 7 and November 9 and 14.

On August 13, 1917, an infected specimen of an *A. radicum* was found on a window.

On August 3, 1916, an epidemic commenced amongst 28 specimens of *S. carnaria* kept in a cage out of doors. Thirteen of the flies died with very well marked signs of the disease on August 3, nine on August 4, and two on each of the three succeeding days.

On August 7 seven wild specimens were caught and placed in the cage. All died of the disease, one on August 9, one on August 10, and five on August 14. Spores were thrown off in the form of a halo round the dead flies (Pl. XIX, fig. 5). Subsequently wild flies of several species were put into this cage, but did not develop the disease. *S. carnaria* therefore seems to be extremely susceptible when exposed to the disease, but the infection of this species has never been recorded previously.

DESCRIPTION OF PLATE XIX.

Fig. 1. Blow fly (*C. erythrocephala*) with a large drop of fluid ("vomit") which had been regurgitated adhering to its proboscis. The drop was subsequently withdrawn. Nat. size.

Fig. 2. *M. stabulans*, sitting on the top of a wall, with a drop of dark coloured, regurgitated fluid adhering to its proboscis. Nat. size.

Fig. 3. Fly with numerous hypopial nymphs adhering to its thorax and head. ×5.

Fig. 4. A specimen of *L. caesar* dead of empusa disease adhering to an artichoke leaf. Nat. size.

Fig. 5. Specimen of *S. carnaria* dead of empusa disease, surrounded by a halo of spores. Nat. size.

Fig. 6. *A. manducator* ovipositing in a larva of *C. erythrocephala*. Nat. size.

Fig. 7. A Figitid emerging from a puparium. ×5.

Fig. 8. Cork of a test-tube in which several specimens of *M. acasta* were confined. Two grooves gnawed by the females are shown (see p. 363). Nat. size.

Fig. 9. Puparia from which *A. cephalotes* emerged (upper row), and from which Figitids emerged (lower row). Nat. size.

Fig. 10. Puparium opened longitudinally showing living nymphs of *M. acasta* (see p. 363). ×4.

Figs. 11, 12. A Proctotrupid (*Trichopria*, sp.) male and female. ×8.

Figs. 13, 14. *M. acasta*, male and female. ×10.

In September 1916 a large number of *M. corvina* confined in another cage outside all died of the disease.

In June 1918 Keilin observed great numbers of *S. stercoraria* dead of the disease clinging to nettles in a meadow near Cambridge.

MITES.

The Gamasid mites previously described (1916, p. 511) were very common on animal remains and faecal matter containing fly larvae during 1916 and 1917, and their habits were more closely observed. They were often seen to attack and kill freshly hatched larvae. They also feed on the eggs of flies, sucking out their contents and rejecting the shrivelled integument. These mites occur in very great numbers, and must cause the destruction of great numbers of eggs and young larvae.

Red mites were seen attached to the legs and bodies of *Lucilia* and *H. dentipes* in July and August in both 1916 and 1917.

BEETLES.

Beetles of various species seriously interfered with several experiments, and are probably beneficial by destroying both larvae and pupae under natural conditions. In one experiment a jar containing fly puparia was left exposed in the open. On examining this jar a few days later 22 specimens of *Creophilus maxillosus* were discovered in it, and almost all the puparia were found to be torn open and destroyed. This beetle is a strong flier, and is readily attracted to all decomposing materials.

Two other species (*Necrophorus humator*, *Hister cadaverrinus*), very common in decomposing animal matter, seem to be destructive to larvae and pupae.

Even buried puparia may be attacked, for in another experiment a large number of puparia buried at a depth of 2 inches were found torn in pieces. One of the beetles (*Pterostichus madidus*) attacking these puparia was closely observed for some time. It carried off a puparium holding it in its mandibles by one end. The puparium was taken from it, and placed on the ground a short distance away. The beetle immediately searched for it, found it, and took it up and finally disappeared with it into a crevice in the ground.

Dr G. W. Nicholson very kindly identified several species of beetles submitted to him.

PARASITES ATTACKING FLY LARVAE OR PUPARIA.

Since the autumn of 1915 fly larvae and puparia collected at various times have been kept under observation in separate receptacles, with notes recording their origin and date of collection. From these naturally infected puparia members of the five most important families of the *Hymenoptera parasitica* or *Terebrantia*, the *Cynipidae*, *Proctotrypidae*, *Chalcididae*, *Ichneumonidae* and *Braconidae*, have been obtained.

These parasites undoubtedly play an important part in restricting the numbers of adult flies which emerge, but hitherto the species parasitic on diptera have been greatly neglected. From their economic importance, the diversity of their habits, and the peculiarities of their structure, these parasites deserve more attention than they have received, and it is with the hope of calling attention to them that the following observations have been recorded. For the same reason a sketch of each species, showing the appearance of the insect, has been inserted. Though such drawings are of no value for determining species, they indicate roughly the characters of insects belonging to different families and illustrate the remarkable diversities of their forms.

Many of the genera embrace scores of species most difficult to identify, and many species are as yet undescribed.

Dr R. C. L. Perkins most kindly examined the examples of the Cynipids and Proctotrupids, Mr J. Waterston several of the Chalcids, Mr C. Morley the Ichneumons and Mr G. T. Lyle the Braconids. Prof. Masi of Genoa, in the absence of Mr Waterston, very kindly identified *Necremnus leucarthros*.

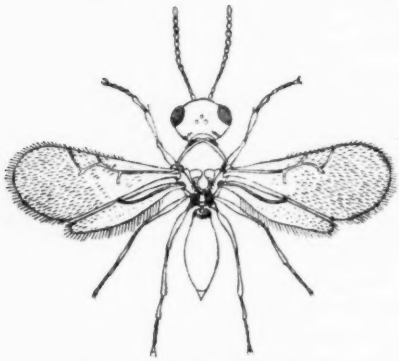

Fig. 1. *Diranchis* sp. ♀. ×20.

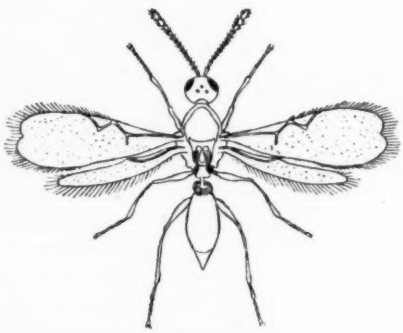

Fig. 2. *Kleidotoma* sp. ♀. ×20.

CYNIPIDAE.

Of this family 4 specimens, 2 ♂ and 2 ♀, of a species of the genus *Diranchis* (Först) emerged in June 1916 from puparia collected in the autumn of 1915.

Five specimens, 3 ♂ and 2 ♀, of a species belonging to the genus *Kleidotoma* (Westwood) emerged in June 1917 from puparia collected in faecal material in the autumn of 1916.

A species of the genus *Figites* emerged in May and June 1916 and 1917 from puparia collected in the preceding years and kept under circumstances which precluded the possibility of spring infection. It was noticed that they appeared from puparia kept outside in a warm situation nearly a month earlier than from puparia kept in the shade. Altogether 73, 28 ♂ and 45 ♀, emerged during these two years. The percentage of infection was very small. For example from one batch of 4280 puparia from larvae feeding on exposed meat only

25 (0·6 per cent.) of these parasites emerged, though throughout the season from June to October the adult parasites were constantly present amongst the larvae, presumably with the intention of ovipositing.

From the exposed carcase of a small animal fluid soon exudes, and in places the surface of the carcase becomes semi-liquid. In these situations very small larvae are numerous. Folds in the skin of the carcase, or crevices in the meat, contain similar material. The Figitids are usually found walking over the semi-liquid material where they may be seen making frequent, quick, stabbing movements with their ovipositors, which are very long and fine. These parasites oviposit in very small larvae only. Sometimes the larvae selected are near the surface and visible, but often they are buried in semi-fluid material and are probably quite invisible to the parasite. In such cases the larvae appear to be discovered with the aid of the ovipositor. The process

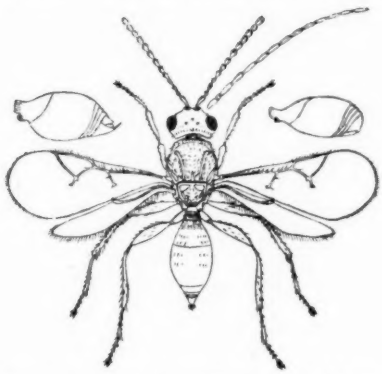

Fig. 3. *Figites* sp. ♀. ×20. ♂ antenna. ♂+♀ abdomen, side view.

Fig. 4. *Figites* sp. ♀. Side view showing position of wings when walking in wet material.

of oviposition occupies 1 to 2 minutes. When in search of larvae amid wet and slimy surroundings or when penetrating into crevices in putrid meat, the Figitids walk in a peculiar manner with the wings folded over the back and the terminal portions bend downwards and closely applied to the dorsal surface of the abdomen. The wings look as if soiled, but this is not the case for on being alarmed they fly off easily, and the position seems to be adopted for the purpose of protecting the wings.

Neither under experimental nor natural conditions were the Figitids seen to attack any but very small larvae. They took no notice of eggs, large larvae or puparia.

Only a single parasite emerged from an infected puparium, and in all the cases observed the puparium was a small one. The opening through which the parasite emerges is irregular (Pl. XIX, figs. 7, 9).

Experimentally this parasite was seen to oviposit over a period of 4 or

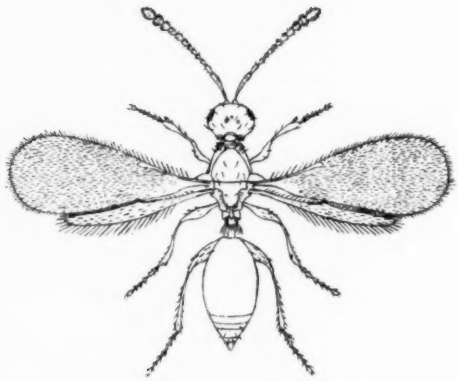

Fig. 5. *Trichopria* sp. ♀. × 20.

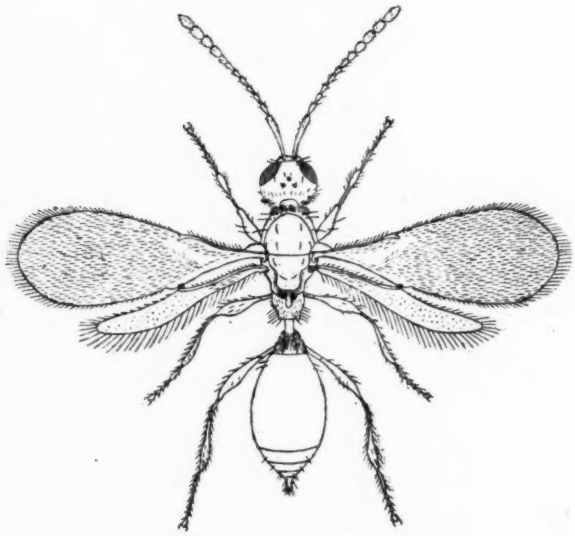

Fig. 6. *Trichopria* sp. ♀. × 20.

5 days. From ova deposited in September 1916 in very small larvae confined in tubes, imagines appeared in June and July 1917.

It will be noticed that all the three species observed passed the winter in fly puparia.

PROCTOTRYPIDAE.

Of this order 4 species were obtained. The commonest was a species of the genus *Trichopria* of which 61 specimens, 15 ♂ and 46 ♀, emerged in June 1917 from puparia collected in the autumn of 1916 from larvae feeding on faecal material. Other specimens emerged in September 1917 from puparia

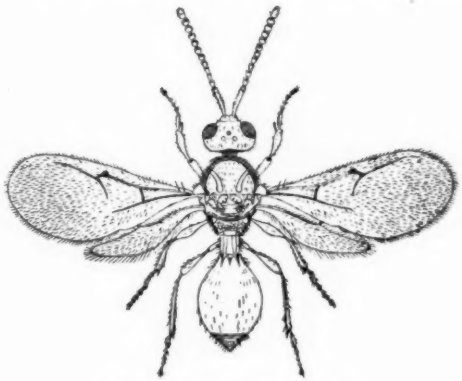

Fig. 7. *Aneurrhynchus* sp. ×20.

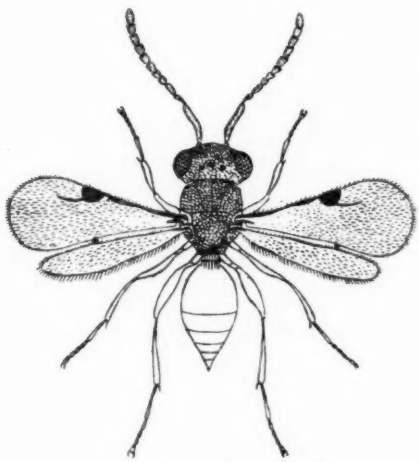

Fig. 8. *Conostigmus* sp. ×20.

collected earlier in the same season. Eleven specimens, 4 ♂ and 7 ♀, of another species of *Trichopria* (? *elongata*, Thoms.) emerged in September 1917 from puparia found in faecal material in June. Very shortly after emerging, many had mites attached to them.

Three specimens of a species of the genus *Aneurrhynchus* appeared in July 1916 from puparia collected in the autumn of 1915 from larvae feeding on

meat, and one specimen of a species of *Conostigmus* or *Lygocerus* in May 1916 from a puparium collected in the autumn of 1915.

These parasites being very small easily escape observation, and it is probable that many species infest the diptera.

ICHNEUMONIDAE.

Only 4 Ichneumons were obtained, all from puparia of *C. erythrocephala*, 1 ♂ *Phygadenon speculator*, Thoms. in July 1916 from a puparium collected earlier in the season, and 1 ♂ and 2 ♀ of *Atractodes bicolor* Gravenh. in June and October 1916 from puparia collected in the summer of 1915 (shade tin).

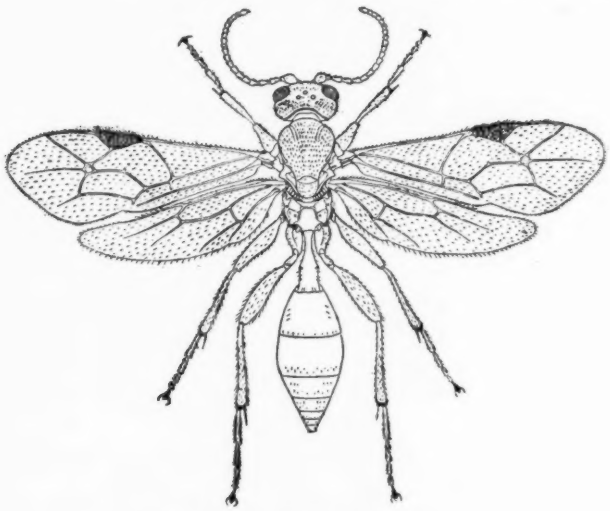

Fig. 9. *Atractodes bicolor* ♀. ×12.

CHALCIDIDAE.

Melittobia acasta Wlk.

Great numbers of fly puparia kept under observation during the winter of 1914–15 were found to be naturally infected by *M. acasta*. "Every puparium attacked by the chalcid was found to be lined by the thick membrane characteristic of a puparium containing a braconid larva." These observations have been quoted in detail (1916, pp. 532–535). At the time of examination (in the winter of 1915–16) a number of intact puparia were discovered from which neither flies, braconids nor chalcids had emerged. Some were dissected and found to contain living chalcid larvae and remains of braconid larvae, but 370 were kept for further observation and placed in jars in a warm room E and a cooler room B. One jar in room E contained 16 puparia, each in a

separate tube. On April 25 2 ♂ *Dibrachys cavus* emerged from 1 puparium. Between May 6 and 19 6 ♂ and 96 ♀ *M. acasta* developed in 12 puparia. Another contained living chalcid larvae and two others dead fly larvae (for details see 1916, p. 543).

On June 10, 1916, 13 puparia were placed in a jar in this room and *M. acasta* commenced to emerge 9 days later. In 11 of these puparia 18 ♂ and 201 ♀ developed.

From the 341 puparia kept in the cooler room B *M. acasta* commenced to emerge at the end of July. In 117 puparia 114 ♂ and 1613 ♀ *M. acasta* developed and *D. cavus* in 9. Six puparia were dissected at various times, and no parasites emerged from the remaining puparia, which were kept under observation for a year and dissected in April 1917. In 101 of these dead specimens of *M. acasta* were found, in 25 living or dead larvae of *A. manducator* and in 83 dead fly larvae or pupae.

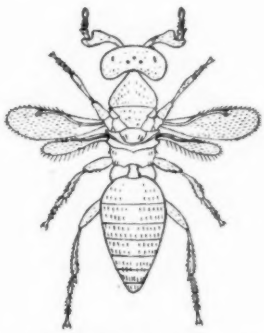

Fig. 10. *Melittobia acasta* ♂. ×20.

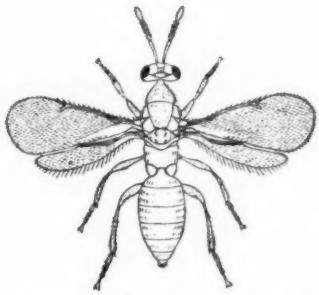

Fig. 11. *Melittobia acasta* ♀. ×20.

These observations show that the emergence of *M. acasta* is greatly hastened by warmth, and that this parasite, when it attacks puparia already parasited by *A. manducator*, may emerge from fly puparia nearly two years old.

It is of interest to note that of the 370 puparia remaining intact after one year's observation 242 or 65 per cent. yielded living or dead adults or larvae of *M. acasta*. Living chalcids, 138 ♂ and 1925 ♀, developed in 140 of the puparia, giving a mean of 1 ♂ and 13 ♀ in each puparium. The mean number emerging from each puparium is small, and this is due perhaps to the fact that all the puparia were previously infected by *A. manducator*.

Similar observations were made with very large numbers of fly puparia kept under identical conditions during the winters 1915–16 and 1916–17. In the former year only one puparium infected with *M. acasta* (1 ♂ and 7 ♀) was observed, and in the latter none. In both years, however, severe infections with other chalcids occurred.

Experiments with M. acasta.

From *M. acasta* which emerged in 1916 several generations were reared on healthy puparia of several species of flies, and some observations made on their habits under these conditions. In most of these experiments the chalcids and the puparia were kept in small corked glass tubes, the contents of which could be examined easily under a binocular dissecting microscope.

Oviposition.

When a ♀ is placed in a tube with a fly puparium she soon begins to walk over it, stopping at frequent intervals and apparently examining the surface. Eventually a place is chosen and the ovipositor applied. During the process of inserting the ovipositor the position of the legs is not changed, but the whole body is raised and lowered rhythmically by movements of the tarsi. At each movement of the body the ovipositor seems to be rotated through a quarter of a circle. Eventually the ovipositor is completely buried. The whole process frequently occupied 2 hours.

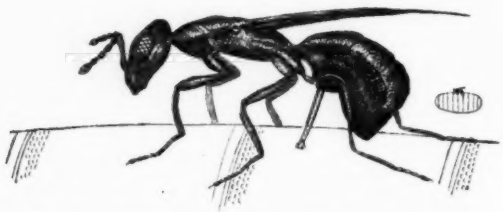

Fig. 12. *Melittobia acasta* ovipositing in a puparium.

One ♀ was seen ovipositing over a period of 48 days and another over a period of 37 days. Fly larvae, whether large or small, did not attract the chalcids, and no attempt was ever made to oviposit in them.

On carefully dissecting a healthy fly puparium a few days after oviposition the eggs of the chalcid, which measure 0·275 × ·0875 mm. and are sticky, are found in groups up to the number of 12, though single scattered eggs are also seen, on the surface of the nymph. The larvae, which emerge from these eggs, remain on the surface of the fly nymph, but become partly imbedded in shallow grooves. Where a puparium already infected by a braconid was attacked only small numbers of chalcid eggs were found lying on the surface of the braconid larva.

The development of M. acasta *larvae.*

The events, which occur during the later stages of the larval life of *M. acasta*, may be followed by opening the infected fly puparia and keeping them in glass topped boxes in the dark. Such opened puparia with *M. acasta* larvae within them have been illustrated previously (Graham-Smith, VIII. 1916, Pl.

XXX, figs. 13, 15 and 16). Three puparia were opened in December 1915 (Graham-Smith, 1916, VIII. p. 543) and kept together in a glass box in a warm room. The *M. acasta* larvae, which were white and glistening, remained almost motionless for five months. On May 22 excrement was deposited, and many of the larvae had changed into white glistening nymphs by May 30. The ♂ nymphs became dark brown in colour and the ♀ nymphs black. This change in colour is gradual, and many of the ♀ nymphs may be white when others have become black. The first ♂ emerged on June 13, and two others in another puparium on June 26. The latter two ♂s fought and one of them killed the other. At this date the ♀ nymphs were still white. Another ♂ emerged on July 9 and was killed by the one which had emerged previously. The surviving ♂s each kept guard over the ♀ nymphs in his own opened puparium. By July 2 two of the ♀ nymphs had become black. The first ♀ emerged on July 17, and shortly afterwards mated with the ♂, which had previously emerged in her puparium. Two ♀s emerged on July 27 and several female nymphs had become black by the time. On July 31 several adult ♀s emerged, but many of the female nymphs were still white.

It is evident from the observations recorded in the following paragraphs that in these opened puparia the events occurred in the same order as they do under natural conditions in intact puparia. The ♂s develop into imagines many days before the ♀s, and fights between them are of frequent occurrence in which the weaker are mutilated, or killed. The survivor remains in the puparium and mates with the ♀s soon after they emerge.

The emergence of M. acasta *from fly puparia.*

The ♀s of *M. acasta* emerge from an intact fly puparium through a small round hole, which one of them gnaws. The hole is usually situated near one end of the puparium, but is occasionally near the centre. Very rarely two such holes are produced in a puparium. (Graham-Smith, 1916, Pl. XXX, fig. 10.) The hole is only just large enough to allow a ♀ to pass out, but is not large enough to admit of the passage of a ♂. Occasionally a ♀ has been seen to re-enter a puparium through such an opening, but usually after they have emerged the ♀s fly away. On one occasion, when the opening was blocked by the body of a ♀ which had died while attempting to emerge, another ♀ which wished to re-enter enlarged the opening from the outside. Since the ♂s are usually too large to emerge through the holes made by the ♀ it is very rare to find one outside a puparium, and they seem to spend their lives within the puparia. This accounts for the large number of bodies of males found within puparia in previous observations (Graham-Smith, 1916, p. 532). The ♀s are fertilised before they emerge from the puparia.

Judging from the behaviour of the parasites when kept in glass tubes only one ♀ is engaged at one time in the work of boring through the puparium, however many there may be within the puparium ready to emerge. This would account for the fact that multiple openings in puparia are very rare

and that numbers of females are often seen emerging one after the other from a puparium through a single opening.

If several ♀s are confined in a corked tube they often endeavour to escape by excavating a tunnel through the cork. In one instance a tunnel 3 mm. long and about 0·5 mm. in diameter (Pl. XIX, fig. 8) was excavated in the part of the cork in contact with the glass, and all the ♀s, 40 in number, escaped through it. In this case, as in many others, the process was carefully watched. Only one ♀ worked at a time, and the others remained quietly cleaning themselves in various parts of the tube. When the worker retired another took her place, and no attempt was made to start fresh channels.

Sometimes though the parasites become adult they fail to emerge from the puparium and die. The cause of this phenomenon has not been ascertained.

Habits of M. acasta.

Males. As mentioned previously the males usually reach the adult condition several days or even weeks before the females in the same puparium. The males vary greatly in size and colour. The largest reaching a length of 2·25 mm. and the smaller specimens only 1·25 mm. They are larger and more stoutly built than the females, but they appear to be blind and owing to their ill-developed wings are incapable of flight. Their colour varies from light yellow to brown.

The males which emerge in opened puparia (see p. 363) remain there though free to get away, if they desire to do so. They sometimes move slowly about amongst the female nymphs, frequently touching them with their antennae and apparently examining them closely, but spend most of their time in cleaning their antennae and legs. If two males emerge in the same puparium they soon meet and fight.

The habits of the males are more easily studied in glass tubes, especially when confined with females. A single male was frequently seen to mate with many females. It may be mentioned that when a male has been present all the females which leave a puparium seem to be fertilised. Though all the movements of the males are slow, and they are seldom in motion for more than a few seconds, their attitude is alert. Especially when in the neighbourhood of other males they walk with the antennae lifted, widely separated, and waving in a peculiar menacing manner. When two males approach one another a fight almost invariably occurs, and a living male has been seen to attack the shrivelled body of a dead male.

Several of these fights were carefully observed. One between two large specimens of almost equal size lasted nearly an hour. Much of the time was occupied in manœuvring to obtain favourable positions. Eventually one specimen was able to get on to the back of the other, and, securing a firm hold with his legs, buried his mandibles in the dorsal part of his adversary's head, and continued to bite for five minutes. During this time the other ceased to

struggle. As soon however as the hold was relaxed the wounded specimen made attempts to get away. In this he was not successful for the first male again succeeded in getting on to his back, and after biting off a wing, buried his mandibles in his opponent's back and bit savagely several times. After this the injured male made great efforts to get away and succeeded. Although he had been badly injured and died within a few hours, he seemed from his actions to be prepared to attack his adversary, if opportunity offered. The victor appeared to be much troubled by the fragments which found their way between his mouth parts, for even during the fight he often tried to remove them by passing his legs between his mandibles and subsequently rubbing them together.

In many instances when several males were placed in a tube all except one were found dead and mutilated within a few hours. On one occasion when a puparium was opened two males were found within, one, though still able to stand, without his head. On another occasion a puparium on being opened contained 13 ♀, 13 female nymphs, and one large, active living male. The mutilated remains of seven other males were also found. Only very rarely was more than one living male found in a puparium.

Females. The females have large eyes and well developed wings, and can fly for a considerable distance. Liberated specimens were often seen to fly for some feet. Usually, however, they only fly for very short distances, one or more inches, in a jerky manner. Their movements are very rapid, unlike the slow movements of the males, and they are very frequently in motion. Much time is spent in cleaning their legs, wings, antennae and bodies, in the same manner and as thoroughly as flies. As previously stated they are apt to burrow through the corks of the tubes in which they are confined, whereas the males never attempt to do so. The females are ready to mate with the males very soon after emerging.

Females, whether fertilised or unfertilised, confined with fly puparia in glass tubes live a long time. The longest periods noted were 95 and 79 days. The mean duration of life of 40 unfertilised females was 36 days and of 18 fertilised females 33 days. These females seem to derive their nourishment from fluid exuding from puparia, which have been punctured by the ovipositor of the parasite.

Experiments with fertilised females.

A number of experiments were carried out with females either derived from puparia containing males or kept in tubes with males. It was presumed that they had been fertilised. In most experiments a single such female was confined in a tube with one or more fly puparia. In some instances the puparia were removed after a few days to other tubes and the female given fresh puparia. In all cases the parasites which emerged were counted, and the puparium subsequently dissected to ascertain the number of males and living female nymphs still present in it. Even when no parasites emerged the puparia

were dissected. The tubes were examined daily and the duration of the life of the female noted.

The results are given in Table II. It will be noticed that female No. 3 was observed to oviposit over a period of 43 days, and produced 7 ♂ and 325 ♀, and 20 ♀ nymphs and No. 16 oviposited over a period of 35 days and produced 4 ♂ and 159 ♀ and 5 nymphs. On the other hand one puparium given to female No. 20 contained only 8 ♀, a puparium given to No. 15 1 ♂ only, and a puparium given to No. 16 1 ♂ and 2 ♀.

The first parasites emerged on the twenty-third and the last on the fiftieth day after the commencement of the experiment. In one case (No. 2) eggs were deposited only in the first puparium which was given, in another (No. 15) only in the second out of three lots of puparia given, in another (No. 16) only in the second and third out of four lots. In some of the experiments the parasites emerged from some of the puparia and were found dead in others. It was common to find dead fly remains, without any trace of the parasites, in dissected puparia possibly indicating that the flies had been killed in some manner by the puncturing of the puparia.

In the course of these experiments 36 ♀ were confined in tubes with 174 fly puparia and in 35 (20 per cent.) of these puparia the parasites developed, and in 2 (1 per cent.) *M. acasta* larvae on dead *A. manducator* larvae were found. From 52 (29·9 per cent.) of the puparia flies emerged, and from 3 (2 per cent.) *A. manducator*. In 76 (43·6 per cent.) dead fly remains and in 6 (3 per cent.) living *A. manducator* larvae were found.

The 33 infected puparia contained 46 ♂, 1335 ♀ and 189 female nymphs, a mean of 1 ♂, 40 ♀ and 6 nymphs in each puparium.

Experiments with virgin females.

In order to secure virgin females for these experiments infected puparia were opened and female *M. acasta* nymphs removed and placed in tubes till they emerged. At varying times after emergence fly puparia were added. Forty-one experiments were carried out, and in each only one female was employed. To these females 225 fly puparia were given. All those puparia from which flies did not emerge were dissected subsequently and the contents noted. In eight instances after the removal of the first batch of puparia a second batch together with a male *M. acasta* was placed in the tube.

From the 225 puparia given to the virgin females 53 (23·5 per cent.) flies, 6 (2 per cent.) *A. manducator* and one Ichneumon emerged. 142 (63·1 per cent.) contained dead fly remains, 16 (7 per cent.) dead *A. manducator* and 3 (1 per cent.) living and 4 (1 per cent.) dead *A. manducator* larvae.

In 15 (7 per cent.) of the puparia one or more male *M. acasta* were found. In eleven instances with dead fly remains, in three with dead *A. manducator* and in one with a dead *A. manducator* larva. Two puparia contained 4 ♂, five 2 ♂, eight 1 ♂. A living *M. acasta* larva was also found on one occasion with dead fly remains. Females were never encountered, and in no case had the

Table II. *Showing results of experiments with fertilised females of* M. acasta.

No. of experiment	No. of females used	No. of puparia given	Age of female in days	Results: Infected puparia	Results: Non-infected puparia	Length of life of female in days
1	1	1	2	(1) 2♂ + 56♀ on 39th day	—	39
2	1	1	2	(1) 1♂ + 12♀ + 47 larvae on 35th day	—	
		1	20	—	(1) dead fly remains	
		1	31	—	(1) fly emerged	37
3	1	1	5	(1) 2♂ + 78♀ + 4 larvae on 36th day	—	
		1	21	(1) 1♂ + 118♀ on 28th day		
		1	31	—	(1) dead fly remains	
		1	37	(1) 4♂ + 129♀ + 16 nymphs		
		1	48	—	(1) fly emerged	50
4	1	2	5	(1) 1♂ + 41♀ on 36th day (2) 1♂ + 17♀ on 43rd day	—	21
5	1	2	2	—	(1, 2) dead fly remains	32
6	1	2	6	—	(1, 2) dead fly remains	42
7	1	2	5	(1, 2) many ♂ + ♀	—	?
8	1	5	5	(1–4) 4♂ + 202♀ + 39 nymphs on 37th to 43rd days	(5) dead fly remains	31
9	1	6	5	(1–6) 8♂ + 190♀ + 9 nymphs on 37th to 50th days	—	33
10	1	6	5	—	(1–5) flies emerged (6) *A. manducator* emerged	21
11	1	6	5	(1) 1♂ + 50♀ (2) 2♂ + 61♀ (3) 1♂ + 51♀ on 41st to 50th days (4) 1♂ + 6♀ (5, 6) 2♂ + 6♀	—	35
12	1	6	5	—	(1–6) dead fly remains	21
13	1	6	5	—	(1, 2) flies emerged (3–6) dead fly remains	21
14	1	6	2	—	(1–2) flies emerged (3–6) dead fly remains	32
15	1	6	2	—	(1–6) dead flies	
		3	22	(1) 1♂ + 59♀ on 28th day (2) 1♂ (3) 5♂ + 10♀ on 23rd day		
		6	36	—	(1–5) flies emerged (6) *A. manducator* emerged	39
16	1	5	5	—	(1) fly emerged (2–5) dead fly remains	
		4	21	(1) 2♂ + 93♀ + 2 nymphs on 31st day (2) 1♂ + 64♀ + 3 nymphs on 26th day	(3, 4) dead fly remains	
		6	31	(1) 1♂ + 2♀	(2–4) flies emerged (5, 6) dead fly remains	
		6	37	—	(1–6) flies emerged	41
17	1	12	5	—	(1–4) flies emerged (5) *A. manducator* emerged (6) *A. manducator* nymph (7–12) dead fly remains	
		12	21	—	(1–9) flies emerged (10–12) dead fly remains	31
18	1	12	2	—	(1–12) dead fly remains	32
19	2	6	5	(1) 44♀ + 31 nymphs (2) 2♂ + 14♀ + 38 nymphs	(3–5) dead fly remains (6) fly emerged	
20	3♀ + 1♂	4	2	(1) 2♂ + 24♀ (2) 8♀	(3, 4) dead fly remains	30
21	13♀ + 1♂	34	4	(1, 2) *A. manducator* larvae with numerous *M. acasta* larvae	(3–14) flies emerged (15–29) dead fly remains (30–34) *A. manducator* larvae living	?

male emerged from the puparium. Consequently it was useless for the female to wait for the male to emerge as happens according to Malyshev (1913) when the parasite infests certain wasp larvae.

In eight instances the first puparia were removed, and a male together with fresh fly puparia added, the additions being made between the seventh and eighty-second days. In four cases (Nos. 4, 9, 10, 11) females, which as virgins produced males, were employed. No further parasites were produced in two of these experiments (Nos. 4, 11), but in the other two a few more of the parasites developed in 3 out of 5 and 2 out of the 6 puparia used. The five infested puparia contained 3 ♂ and 16 ♀, 6 ♂ and 14 ♀, 1 ♂ and 19 ♀, 1 ♂ and 6 ♀ and 1 ♂ and 6 ♀ respectively. In four cases females (Nos. 8, 12, 17, 18), which as virgins produced no males, were employed. Not a single parasite was found in the 24 puparia used.

One of the females lived 95 days, 14 lived more than 40 days. The mean length of life was 35 days.

In another experiment carried out in 1917 a remarkable number of males developed. Seven unfertilised females were given six fresh fly puparia. In two of these 6 ♂ were found, in one 4 ♂, and in one 2 ♂, a mean of 4·5 ♂ for each infected puparium.

Howard and Fiske (1912, p. 209) were greatly troubled with *M. acasta* in some of their experiments with tachinids, and report some interesting observations. Its chief characters are "extreme hardiness and an insidious inquisitiveness, which seems to know no bounds." These parasites attacked several different kinds of fly puparia as well as hymenopterous cocoons. "They will enter the damp earth to a depth of several inches in quest of puparia, which have been buried therein." "The eggs are deposited upon the surface of the nymph in an irregular circle surrounding the wound made by the ovipositor. They are very small and appear to swell somewhat before hatching, and if the puparium is broken open so that they are freely exposed to the air, they will fail to hatch." They noted that the male emerged first and state that "they are invariably in the great minority and their numerical strength is still further reduced by the terrific duels which follow their emergence. Notwithstanding their physical defects in the matter of sight and powers of flight, their seeming weakness otherwise and their small size, even when compared with their mates, they possess a courage and vigour which is most surprising. In the instance of a colony which had been removed, from the puparium in which it was reared through its early stages, to a small glass cell, the several males which issued well in advance of the females engaged forthwith in conflict, in the course of which a considerable number were killed. The survivors of this Lilliputian battle royal calmly awaited the issuance of the members of their harems and proceeded to mate with one and all with an ardour which seemed to know no limit."

"The females (virgin) positively refused to deposit more eggs than would have normally produced males had they been properly fertilised. Instead of

Table III. *Showing results of experiments with virgin females of* M. acasta.

No. of experiment	No. of females used	No. of puparia given	Age of female in days	Result	Male placed in tube	No. of puparia given after male added	Result	Length of life of female in days
1	1	1	6	dead fly remains + 2♂	—	—	—	60
2	1	1	6	dead fly nymph	—	—	—	7
3	1	1	7	dead fly nymph + 1♂	—	—	—	42
4	1	1	5	dead fly nymph + 1♂	82nd day	5	dead fly remains in all	95
5	1	2	6	(1) dead fly nymph (2) dead *A. manducator*	—	—	—	23
6	1	2	6	dead fly remains in both	—	—	—	42
7	1	2	7	(1) dead *A. manducator* + 2♂ (2) dead *A. manducator* + 2♂	—	—	—	79
8	1	4	4	(1) fly emerged (2, 3, 4) dead fly remains	14th day	5	dead fly remains in all	21
9	1	5	4	(1, 2) flies emerged (3) dead fly remains (4) dead fly remains + 2♂	14th day	5	(1) 1♂ + 19♀ (2) 1♂ + 6♀ (3) 1♂ + 6♀ (4, 5) dead fly remains	22
10	1	5	6	(1) fly emerged (2, 3, 4) dead fly remains (5) dead fly remains + 1 *M. acasta* larva	13th day	6	(1) 3♂ + 16♀ (2) 6♂ + 14♀ (3, 4, 5) flies emerged (6) dead fly remains	26
11	1	6	5	(1) fly emerged (2, 3, 4, 5) dead fly remains (6) dead fly remains + 1♂	14th day	8	(1, 2, 3, 4) flies emerged (5, 6, 7, 8) dead fly remains	32
12	1	6	3	(1, 2, 3) flies emerged (4, 5, 6) dead fly remains	14th day	6	(1, 2, 3) flies emerged (4, 5, 6) dead fly remains	21
13	1	6	2	(1, 2) flies emerged (3, 4, 5, 6) dead fly remains	—	—	—	11
14	1	6	5	(1, 2) flies emerged (3, 4) dead fly remains (5, 6) braconid larvae	—	—	—	28
15	1	6	6	(1, 2) dead fly remains (3) dead fly remains + 1♂ (4) dead braconid larva + 1♂ (5) *A. manducator* emerged (6) *A. manducator* dead	—	—	—	54
16	1	6	1	(1) *A. manducator* dead (2, 3, 4, 5, 6) dead fly remains	—	—	—	25
17	1	6	1	(1) Ichneumon emerged (2, 3, 4) flies emerged (5, 6) dead fly remains	7th day	6	(1–6) flies emerged	15
18	1	6	3	(1–6) dead fly remains	11th day	6	(1) fly emerged (2) *A. manducator* emerged (3, 4, 5, 6) dead fly remains	27
19	1	6	6	(1) *A. manducator* emerged (2) dead fly remains + 1♂ (3, 4, 5, 6) dead fly remains	—	—	—	?
20	1	6	8	(1–2) flies emerged (3, 4, 5, 6) dead fly remains	—	—	—	52
21	1	6	8	(1–6) dead fly remains	—	—	—	40
22	1	6	8	(1) fly emerged (2–6) dead fly remains	—	—	—	49
23	1	6	8	(1–6) dead fly remains	—	—	—	55
24	1	6	8	(1–4) flies emerged (5–6) dead fly remains	—	—	—	49
25	1	6	8	(1–4) flies emerged (5–6) dead fly remains	—	—	—	53
26	1	6	6	(1–6) dead fly remains	—	—	—	49

Table III (*continued*).

No. of experiment	No. of females used	No. of puparia given	Age of female in days	Result	Male placed in tube	No. of puparia given after male added	Result	Length of life of female in days
27	1	6	6	(1) fly emerged (2) *A. manducator* emerged (3–6) dead fly remains	—	—	—	19
28	1	6	6	(1–3) flies emerged (4) *A. manducator* nymph (5) dead fly remains (6) dead fly remains + 1 ♂	—	—	—	37
29	1	6	6	(1) *A. manducator* emerged (2–6) dead fly remains	—	—	—	30
30	1	6	6	(1–2) flies emerged (3) *A. manducator* emerged (4–6) dead fly remains	—	—	—	37
31	1	6	6	(1) fly emerged (2–5) dead fly remains (6) dead *A. manducator*	—	—	—	28
32	1	6	6	(1–3) flies emerged (4–6) dead fly remains	—	—	—	22
33	1	6	6	(1–2) flies emerged (3–4) dead fly remains (5) dead fly remains + 1 ♂ (6) dead fly remains + 4 ♂	—	—	—	37
34	1	6	6	(1–3) flies emerged (4–5) dead fly remains (6) dead fly remains + 4 ♂	—	—	—	30
35	1	6	6	(1–2) flies emerged (3–6) dead fly remains	—	—	—	30
36	1	6	6	(1–6) dead fly remains	—	—	—	19
37	1	6	6	(1–5) dead fly remains (6) *A. manducator* larva	—	—	—	25
38	1	6	6	(1–2) flies emerged (3–4) dead fly remains (5) dead fly remains + 2 ♂ (6) dead *A. manducator*	—	—	—	35
39	1	9	?	(1–5) flies emerged (6) dead fly remains (7) *A. manducator* dead (8–9) *A. manducator* larvae	—	—	—	58
40	1	12	6	(1–3) flies emerged (4–8) dead fly remains (9–11) *A. manducator* dead (12) *A. manducator* emerged	—	—	—	31
41	1	12	6	(1–10) dead fly remains (11–12) dead *A. manducator*	—	—	—	23

depositing sufficient to provide for the complete consumption of the host, only four or five would be deposited at a time, and notwithstanding that after the depositing of what probably amounted to barely 5 per cent. of those which filled their abdomens fairly to bursting, they ceased, and nothing short of impregnation seemed to arouse their maternal instincts again." "This progeny, as was expected, was exclusively of the male sex, which when afforded opportunity, promptly united with their virgin mothers, who thereupon displayed the normal desire to deposit their eggs." From such eggs both sexes were reared.

Malyshev (1913) made some very interesting observations on the habits of *M. acasta* as a parasite of solitary wasps. He states that the females can only fly 1–2 mm. The females frequently wound the wasp larvae with their ovipositors and suck the wounds. Such larvae never moult, make a cocoon or transform, but are immobilised and finally die, though very slowly. The females lay 200–300 eggs, or perhaps more. The males emerge first and fights ensue in which some are decapitated or loose their legs or abdomens. He notes that virgin females only lay four or five eggs, which give rise to males. Such females then wait in the neighbourhood and eventually mate with the males which emerge, and within 24 hours lay numerous eggs. The males never leave the nests in which they were hatched. He states that *M. acasta* attacks the

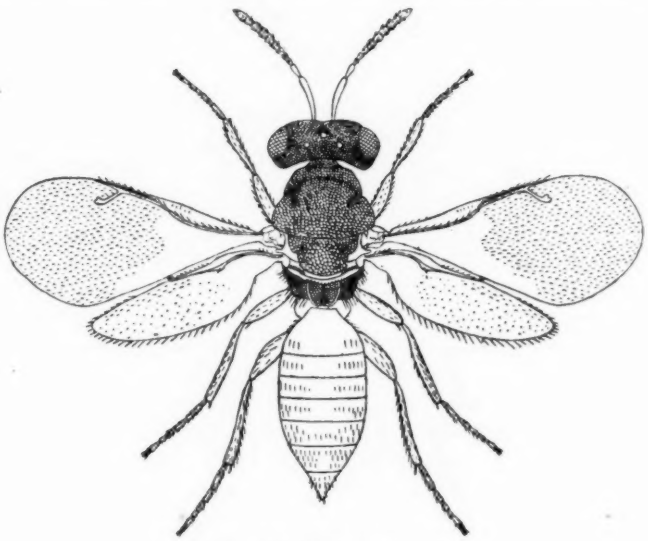

Fig. 13. *Dibrachys cavus* ♀. ×20.

tachinids which parasitise the wasps. They never lay their eggs on the tachinid (*P. signatus*) larvae, which are very lively, but wait till they pupate and oviposit on the puparia.

Dibrachys cavus.

D. cavus was first encountered in small numbers in puparia collected in the autumn of 1914. From thirteen of these 37 of the parasites emerged in April and May 1916. Fly puparia collected in the autumn of 1915 showed however heavy infection with this parasite. Some of these parasites emerged in September 1916, namely 19 ♂ and 65 ♀ from 15 puparia. The remainder did not commence to emerge till March or April 1917. Then 433 *D. cavus* emerged from 154 puparia, the sexes being nearly equal in numbers. The numbers

ranged from 2 to 9 from each puparium. Some of the jars in which the fly puparia were kept were covered with cloth in January 1916 and in these no chalcids were found. Consequently the infection occurred in the spring of 1916. All these chalcids occurred in puparia parasitised by *A. manducator*, but it is probable that at the time infection took place no normal puparia were present, the flies having already emerged. Experimentally *D. cavus* oviposits in the normal puparia of many common flies, including *M. stabulans* and *P. greenlandica*. The process is very similar to that which occurs in the case of *M. acasta*. *D. cavus* in emerging makes a round opening much larger than that made by *M. acasta*, which may be situated in any part of the puparium.

Several experiments were carried out in which females together with males of *D. cavus* were confined in tubes with fly puparia. In one 15 puparia were used. In four of these puparia 5 ♂ and 45 ♀ emerged; one contained dead adults and 10 dry fly remains. A single fertilised female was confined with a different puparium on consecutive days. From six of these 6 ♂ and 50 ♀ emerged. This parasite therefore seems to be less prolific than *M. acasta*.

In another experiment 16 of the chalcids, males and females, were confined in one tube with eight fresh fly puparia. The parents were all dead by the seventeenth day, and the new generation began to emerge on the thirty-sixth day. Altogether 20 ♂ and 63 ♀ emerged, giving a mean of 2 ♂ and 8 ♀ for each puparium. One puparium contained 2 ♂ and 12 ♀, another 5 ♂ and 9 ♀ and another 4 ♂ and 11 ♀. All the puparia were parasitised.

Nasonia brevicornis.

This chalcid was first obtained from puparia collected in the summer of 1916, and emerged at the end of April 1917. From 16 puparia, unparasitised by *A. manducator*, 14 ♂ and 167 ♀ emerged, a mean of 11 chalcids to each infected puparium. Puparia collected in the autumn of 1916 and kept outside yielded in May 1917 38 ♂ and 369 ♀. Some of these autumn puparia had been parasitised by *A. manducator*. The proportion of males to females was therefore about 1 to 10 in each instance. Some of these autumn puparia remained intact, and were dissected in March 1918. Of these 28 were found to contain living chalcid larvae and were kept in tubes in a warm room. Nineteen of these 28 showed infection with *A. manducator*. Adult *N. brevicornis*, 11 ♂ and 48 ♀, emerged in May 1918, a year and a half after the puparia were collected.

Both the males and females show great variations in size, some of the former being very small and many of the latter very large. The males have very short wings and are unable to fly. Unlike the males of *M. acasta* they emerge from the fly puparia, and run rapidly amongst the earth and debris and are difficult to find and catch. As in the case of *D. cavus* the hole through which the chalcids emerge may be situated in any part of the puparium.

Ten females confined in a tube on April 30, 1917, with 19 puparia were all dead in 13 days. From 16 of these puparia 24 ♂ and 156 ♀ emerged between the twenty-fourth and twenty-ninth days from the commencement of the

experiment. The remaining three puparia contained dead fly remains. The greatest number of the parasites from one puparium was 2 ♂ and 11 ♀.

In a second experiment six of the chalcids were confined in a tube with 12 puparia on May 1, 1917. All were dead within 15 days. 29 ♂ and 102 ♀

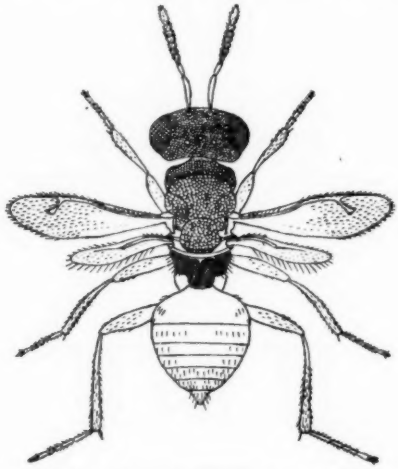

Fig. 14. *Nasonia brevicornis* ♂. ×20.

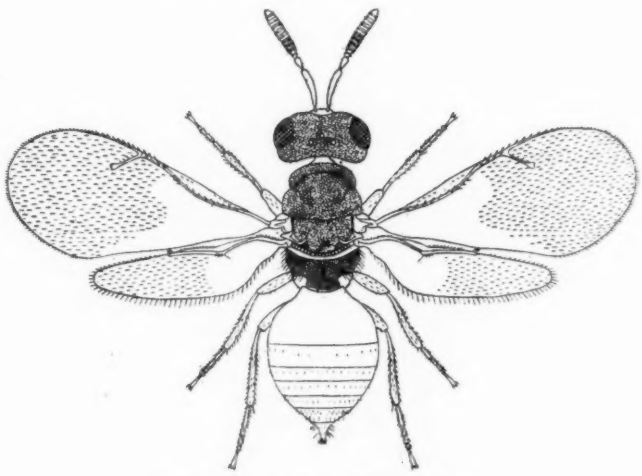

Fig. 15. *Nasonia brevicornis* ♀. ×20.

emerged within 47 days of the commencement of the experiment. On dissecting these puparia 10 chalcid nymphs were found also.

In a third experiment six females were confined with 12 puparia on May 1. Within 30 days 14 ♂ and 70 ♀ emerged from six of the puparia. From

one of these puparia 3 ♂ and 12 ♀ emerged. The others were subsequently dissected and found to contain dead fly remains.

In a fourth experiment two females were confined with six puparia on May 3, 1917. 4 ♂ and 39 ♀ emerged on May 28 from three of the puparia. On dissecting the remaining puparia one dead male, two dead females and 10 dead nymphs were found in one, several dead chalcid larvae in another, and dead fly remains in the third.

In a fifth experiment a single female was confined with three puparia on May 1. From these puparia 7 ♂ and 27 ♀ emerged on the twenty-sixth day.

In these experiments 40 infected puparia yielded 78 ♂ and 394 ♀, a mean of 2 ♂ and 10 ♀ from each puparium; the number emerging from each puparium

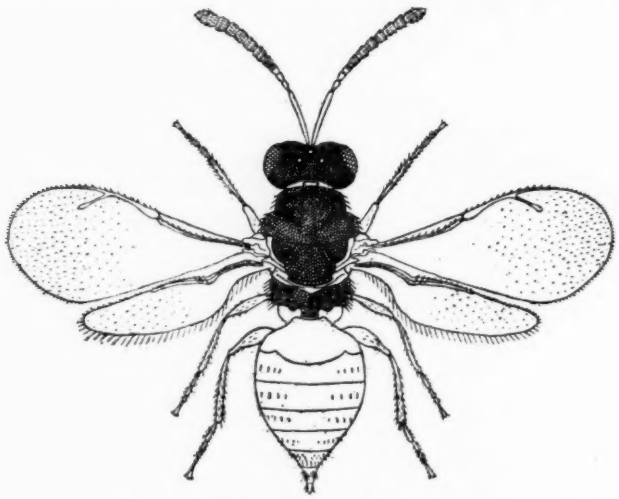

Fig. 16. *Muscidifurax raptor* ♀. ×20.

being almost the same as from the naturally infected puparia. In this chalcid the proportion of males to females is much greater than in *M. acasta*, and the number of eggs deposited in each puparium much less.

Muscidifurax raptor.

A few specimens of the chalcid, 3 ♂ and 12 ♀, emerged between August 23 and September 26, 1917, from puparia collected during July of that year.

Five ♀ to which 20 fly puparia were given lived 40 to 50 days. From two of the puparia single females emerged, the other 18 containing dry fly remains.

Necremnus leucarthros Thoms.

Six examples of this chalcid, 1 ♂ and 5 ♀, emerged between August 5 and September 3, 1917, from puparia collected earlier in the summer.

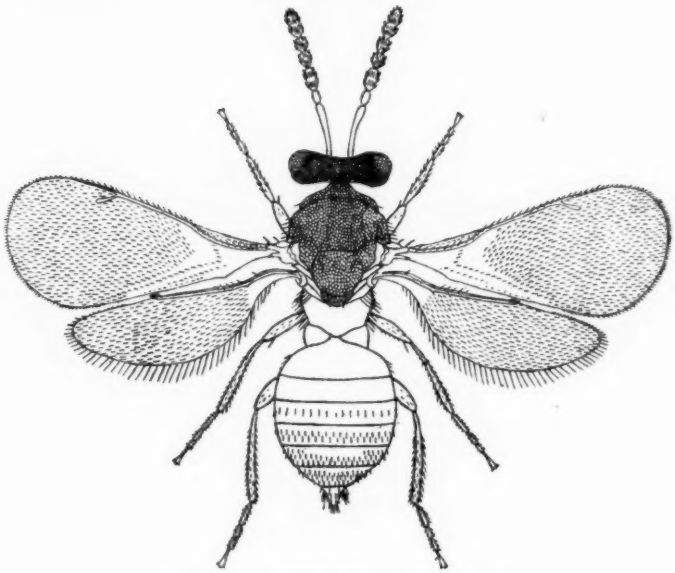

Fig. 17. *Necremnus leucarthros* ♀. ×20.

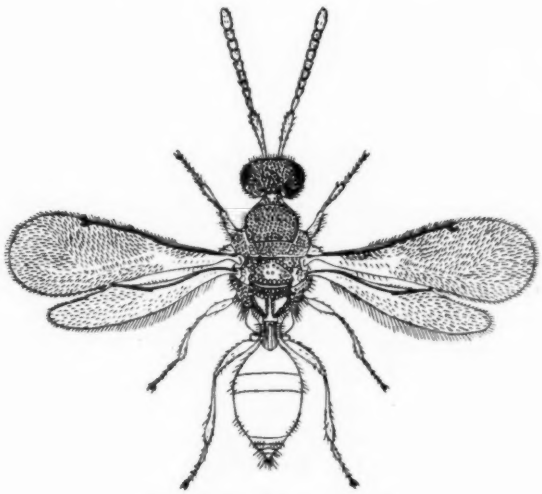

Fig. 18. *Spalangia hirta*. ×20.

Spalangia hirta Hal.

A specimen emerged on August 5, 1917, from puparia collected on July 5, 1917.

Stenomalus muscarum.

This chalcid was not obtained from fly puparia, but in view of the fact that it has been found hibernating in company with flies on several occasions some observations on its seasonal prevalence may be of interest. In 1916 large numbers were present on the windows on March 3 and 18. Few were noticed during the summer, but hundreds were observed on the windows on September 27 and 28, October 1 and 2, and November 15. In 1917 a few were noticed on the windows on April 7, 20 and 29 and very large numbers on September 6, 24 and 29. In 1918 they were numerous on the windows on March 25. Attempts were made to induce females to oviposit in fly puparia, but without success.

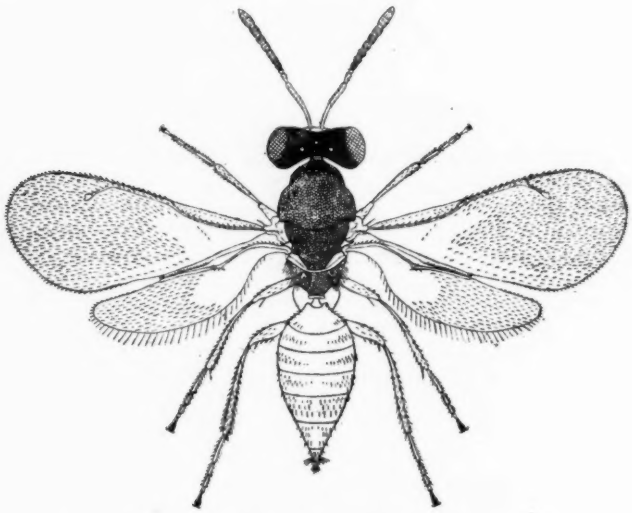

Fig. 19. *Stenomalus muscarum* ♀. ×20.

BRACONIDAE.

Alysia manducator.

A. manducator has been obtained in considerable numbers each year from several series of fly puparia bred under natural conditions.

The observations made in 1915 and previously recorded (1916, p. 524) showed that numerous specimens of *A. manducator* emerged from puparia collected from shady situations in the autumn of 1914. A small batch consisting of 209 specimens appeared in the spring of 1915, and after an interval of three months a second and larger batch of 1115 specimens, being 83 per cent. of the total number. Of all the puparia collected 61 per cent. were infected by this parasite. Further it was shown that the time of emergence in the spring

is greatly influenced by the temperature at which the parasitised fly puparia are kept (1916, p. 531).

Fly puparia collected from small carcases lying (*A*) in sunny, and (*B*) shady situations during the autumn of 1915 were placed in boxes covered with fine gauze, which were left during the following winter at the breeding places. From these puparia very numerous examples of *A. manducator* emerged during 1916.

Situation	No. of fly puparia	*A. manducator* Spring batch 9 April—30 May	*A. manducator* Autumn batch 13 Sept.—15 Nov.	Subsequent examination of puparia remaining intact. *A. manducator* Dead adults	Living larvae
A, sunny	4742	673 ♂ + 159 ♀	148 ♂ + 43 ♀	179	9
B, shady	5163	158 ♂ + 140 ♀	1912 ♂ + 447 ♀	290	41

At least 25 per cent. of the puparia from the sunny situation and 57 per cent. of those from the shady situation were infected with *A. manducator*, but while from the sunny situation 81 per cent. of the parasites emerged in the spring, from the shady situation 83 per cent. of them emerged in the autumn. In each situation more than three-quarters of all the specimens were males, and it was noticed that a large proportion of the males emerged before the females commenced to appear both in the spring and autumn batches. In the sunny situation between April 9 and May 9 471 ♂ and only 26 ♀ emerged, and in the shady situation between September 27 and October 16 1416 ♂ and only 140 ♀. Possibly the predominance of males is due to the fact that virgin females very readily deposit eggs which produce males (see p. 380).

From the puparia mentioned there also emerged:

Situation	Living flies	Dead flies*	Puparia containing *A. cephalotes* Living	Puparia containing *A. cephalotes* Dead*	*Figitids*	*D. cavus* Adults	*D. cavus* Larvae*
A, sunny	1040 ♂ + 1107 ♀	989	192	122	5	13	62
B, shady	843 ♂ + 677 ♀	501	26	6	25	2	93

* The puparia remaining intact were dissected nearly a year later.

In this instance secondary chalcid infection exerted little influence on the results. Occasionally, however, secondary chalcid infection has a great influence on the numbers of *A. manducator* emerging in the autumn. Such an instance has been illustrated in detail previously (1916, pp. 533–535), puparia infected with *A. manducator* in the "sun tin" being attacked by *M. acasta*, while those in the "shade tin" escaped. In the former during the autumn numerous chalcids emerged but not a single *A. manducator*, while in the latter more than a thousand *A. manducator* appeared, but no chalcids.

It may be of interest to inquire how far the appearance of the spring and autumn batches is influenced by temperature. Some puparia collected in the autumn of 1915 were kept in rooms at different temperatures. In the three cooler rooms both spring and autumn batches appeared, but in the three warmer rooms spring batches only. Since the latter rooms were very warm

and dry the larvae due to produce imagines in the autumn may have been killed, and the single experiment is not conclusive.

Fly puparia collected in the autumn of 1916 from a sunny situation were kept under observation throughout 1917 with the following results:

			A. manducator				*A. cephalotes*	
Puparia	Flies emerged	Dead flies*	Spring	Autumn	Dead*	Larvae*	Living	Dead*
3245	230	1351	384 ♂ + 379 ♀	51 ♂ + 21 ♀	681	2	20	8

N. brevicornis			
Living	Dead*	Larvae*	*Figitids*
69	15	28	6

* The puparia remaining intact were dissected nearly a year later.

In 1917 the spring was very cold until the end of April, but after that date the weather was very hot, and possibly it was due to this that so many of the fly nymphs and braconid larvae died.

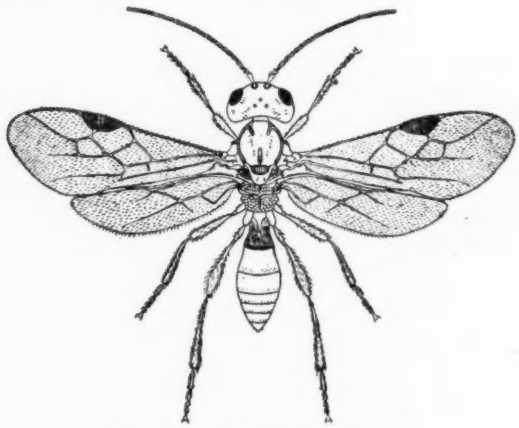

Fig. 20. *Alysia manducator* ♀. ×5.

In this instance as in 1916 the great majority (90 per cent.) of the specimens of *A. manducator* which emerged did so in the spring. Of the fly puparia at least 1565 (48 per cent.) were infected with *A. manducator*, namely 1518 in which the braconid was found and 47 secondarily infected by *N. brevicornis*.

At various times during the summer months of 1916 4280 puparia were collected from animal remains, and from these both the flies and their parasites emerged during the same season.

			A. manducator					
Puparia	Flies emerged	Dead flies	Emerged	Dead	Larvae	*A. cephalotes*	*Figitids*	*Chalcids*
4280	2996	506	151 ♂ + 99 ♀	77	11	3738 from 415 puparia	25	0

Only 8 per cent. of these puparia were infected with *A. manducator*.

In 1917 2188 fly puparia were collected on July 5 from similar situations.

Puparia	Flies emerged	Dead flies	*A. manducator*		*N. brevicornis*	
			Emerged	Dead	Adults from	Larvae in
2188	1791	277	13 ♂ + 17 ♀	23	59	8

Only 2 per cent. of these puparia were infected with *A. manducator.*

Of the 16,028 puparia collected in the autumns of 1914–15–16 from sunny and shady situations 7041 or 43 per cent. were infected with *A. manducator,* while of the 4787 puparia collected during the summer months of 1916–17 only 508 or 10 per cent. were infected.

These observations seem to indicate that infection with *A. manducator* is much greater in the autumn than during the summer. The parasite, however, is abundant throughout the season for it was observed attacking fly larvae from May 30 to November 1, 1916.

Observations on the habits of A. manducator.

Females were often kept under observation when depositing their eggs under natural conditions. The larger larvae seem to be selected for attack. The parasite seizes the larva with its legs, and in spite of the violent struggles of the victim, during which the pair turn over and over, seldom releases its hold. The struggle usually lasts several seconds. Finally the ovipositor is inserted and very soon afterwards the larva ceases to struggle, and remains motionless. The ovipositor remains inserted for 40–50 seconds, and is then withdrawn. After a period of one or two minutes the larva begins to move again and eventually regains full activity. As soon as the parasite leaves one larva it attempts to attack another. After a time it becomes battered and feeble and is only able to move slowly, owing to its struggles with a succession of larvae.

The parasites usually seem to be able to secure a better hold on larvae moving towards them than on larvae moving away from them, for the former very seldom escape, while the latter occasionally do so.

The ovipositor may be inserted into the anterior or posterior end of the larvae or more rarely into the middle.

Sometimes the parasites walk over masses of large larvae, select several and oviposit in them. Occasionally they oviposit in larvae feeding under a thin shell of meat, driving their ovipositors through the shell and ovipositing without seizing the larvae.

While males kept in confinement sometimes remain alive for 15 days, females confined with larvae, even though provided with places on which they can rest, invariably die in three or four days.

Experiments with A. manducator.

A large fertilised female *A. manducator* was put into a jar with 544 large fly larvae, chiefly *C. erythrocephala.* The parasite was found dead on the

fourth day. On dissecting the body 343 eggs were found in the ovaries. Of the larvae 80 died, possibly due to infection by the insertion of the ovipositor (see Fabre, p. 408). From 170 puparia flies emerged within 25 days and from 193 there emerged 47 ♂ and 146 ♀ *A. manducator* between the thirtieth and ninety-fifth days. The remaining 101 puparia were examined on the hundred and seventieth day; 88 contained dead fly remains, 5 dead adult *A. manducator* and 8 dead *A. manducator* larvae. In this case the female *A. manducator* deposited eggs in at least 206 of the larvae provided.

Under more natural conditions it is likely that she would have infected a greater number as the ovaries contained at least 549 eggs.

In another experiment a fertilised female *A. manducator* was given 58 large larvae in succession, and was seen to insert its ovipositor into each in turn. All these larvae pupated. From five flies emerged on the twenty-fifth day, and from 28 of them 10 ♂ and 18 ♀ *A. manducator* between the thirty-fifth and ninety-fifth days. The remaining 25 puparia were examined on the hundred and seventieth day. Seven contained dead fly remains and 18 dead adults or larvae of *A. manducator*.

In this case all the parasitic eggs were deposited on the same day in larvae of the same age, which were kept under identical conditions, yet the first adult *A. manducator* emerged on the twenty-fifth day and the last on the ninety-fifth day. All the 10 ♂ and 4 of the ♀ emerged between the twenty-fifth and thirty-seventh days, and the other 10 ♀ between the sixty-first and ninety-fifth days.

In a third experiment a fertilised female *A. manducator* was placed in a glass jar and four large fly larvae introduced. The parasite soon oviposited in each larva and after an interval when the larvae began to move about attacked each a second time. The experiment was repeated until she had apparently oviposited twice in 19 larvae. Five of these larvae died, and the other 14 pupated. From one a fly emerged on the twenty-fifth day. 2 ♂ and 1 ♀ *A. manducator* emerged on the thirty-first, forty-second and forty-third days and 4 ♀ between the seventy-first and eighty-fourth days. The six remaining puparia were examined on the hundred and seventieth day. Three contained dead fly pupae, one a dead *A. manducator* and two dead *A. manducator* larvae.

This experiment shows that flies may sometimes develop from larvae in which the parasite has presumably deposited two eggs and that from such larvae only single specimens of *A. manducator* emerge.

In a fourth experiment an unfertilised female *A. manducator* was placed in a jar with 191 large fly larvae. She was found dead on the fourth day, and on dissection only 17 eggs were found in the ovary.

Of the larvae 76 died and the rest pupated. From these 19 flies emerged on or before the twenty-first day. Between the forty-first and forty-seventh day 42 ♂ and between the seventy-second and seventy-ninth 29 ♂ of *A. manducator* emerged. The remaining 25 puparia were examined on the hundred and seventieth day. Dead fly remains were found in 13 and dead *A. manducator* in 12.

This experiment shows that unfertilised females oviposit readily, and that large numbers of males only are produced. As noticed in all other cases there were two distinct periods of emergence.

From larvae first attacked by *A. cephalotes* and subsequently by *A. manducator* only *A. cephalotes* emerged.

A. manducator were never seen to attack larvae feeding on faecal material.

Aphaereta cephalotes Hal.

Numerous specimens of *A. cephalotes* have been reared from naturally infected puparia kept throughout the winter in glass jars. About 10 adults in the proportion of 2 ♂ to 8 ♀ emerge from the larger puparia. This parasite usually begins to emerge from over wintered puparia at the end of April and continues to emerge throughout May. There is no autumn batch such as occurs in the case of *A. manducator*.

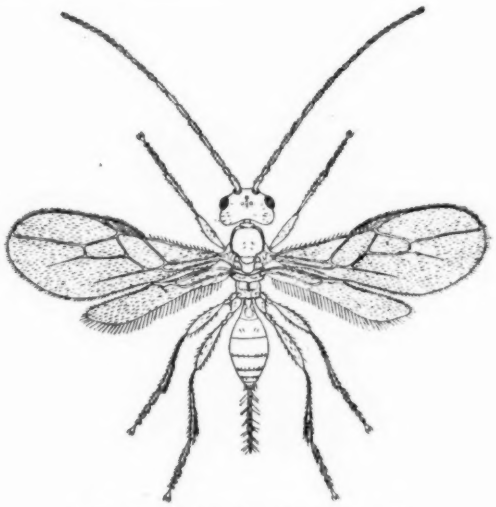

Fig. 21. *Aphaereta cephalotes* ♀. ×10.

Out of 4742 puparia from a sunny situation kept under observation in the winter 1915–16, 314 (6 per cent.) were infected with *A. cephalotes* and produced 2496 individuals, whereas of the 5163 puparia from a shady situation only 32 (0·6 per cent.) were infected with *A. cephalotes*.

A. cephalotes seems to be afraid of the larger larvae and can hardly be induced to attack them even when no other larvae are present, but it oviposits very readily in small fly larvae. The procedure of the parasite when ovipositing resembles that of *A. manducator*, but the ovipositor is inserted for a much longer period, in one case as long as 7 minutes, and the larvae remain motionless longer, up to 30 minutes.

Both exposed larvae and those hidden under folds of skin, etc., are attacked. The parasite frequents such situations and often inserts its abdomen into clefts and seems to feel for hidden larvae with its ovipositor.

At least from some puparia the males emerge first. For example from one puparium 2 ♂ emerged and on examining the contents of the puparium 2 ♀ nearly fully developed were found and several female nymphs.

Occasionally only one or two of these parasites develop in a puparium, and these are often very large.

This parasite frequents both animal remains and faecal material throughout the summer and autumn.

Aspilota fucicornis Hal.

Several specimens of this small braconid were reared in August, 1917, from puparia found in excrement in July.

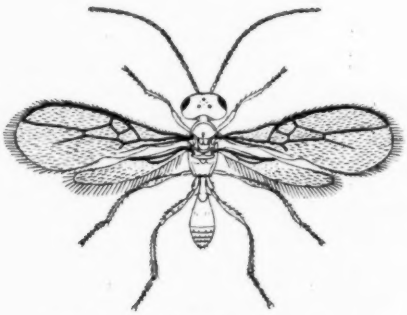

Fig. 22. *Aspilota fucicornis.* ×15.

Aspilota nervosa Hal.

A single specimen emerged in the spring of 1917 from puparia collected in the previous autumn.

CONCLUSIONS.

1. In the year 1915 flies caught in a trap baited with excrement were most abundant in August and September, in 1916 in July and in 1917 in May and June. In each year the curve indicating the number of flies caught corresponds with the curve for the maximum temperatures recorded by a thermometer exposed in the sun.

2. Flies spend a very large proportion of their time in cleaning themselves, and the procedures usually follow each other in a definite order.

3. Empusa disease occurs in several species of flies. Specimens of *C. erythrocephala, L. caesar, H. dentipes, F. canicularis, A. radicum, S. carnaria, M. corvina* and *S. stercoraria* suffering from the disease have been noticed.

4. Certain Gamasid mites destroy both fly eggs and young larvae.

5. Certain species of beetles destroy large numbers of fly puparia.

6. Numerous parasites were obtained from naturally infected fly puparia. Most of these over-wintered in the puparia. The parasites include numbers of the five most important families of the *Hymenoptera parasitica* or *Terebrantia*, namely the *Cynipidae*, *Proctotrypidae*, *Ichneumonidae*, *Chalcididae* and *Braconidae*. Infection with species belonging to the last two families is very common.

7. In 1915 great numbers of the chalcid *M. acasta* emerged from naturally infected fly puparia. Experiments and observations on these parasites showed that they frequently parasitised puparia already infected with the braconid, *A. manducator*. The males, which are blind, unable to fly and relatively few in numbers, reach maturity before the females in the same puparia, and the stronger specimens destroy the weaker. The males never leave the puparia in

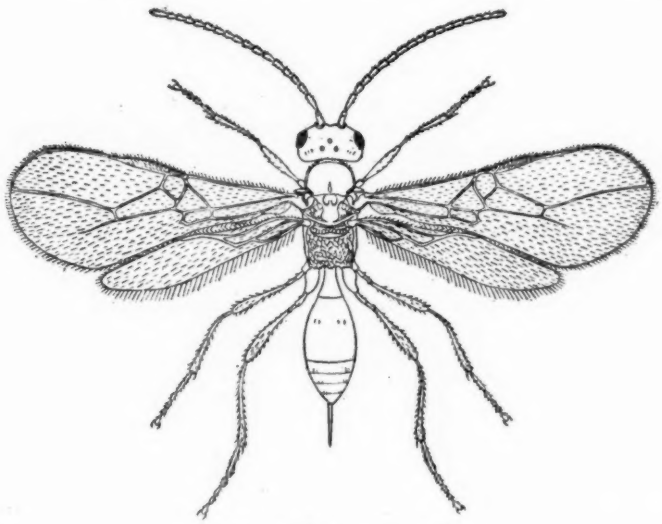

Fig. 23. *Aspilota nervosa*. ×10.

which they emerge, but mate with the females before the latter escape from the puparia. Fertilised females lay large numbers of eggs from which a few males and numerous females develop, but virgin females only lay a few eggs from which males develop. If fertilised subsequently numerous eggs are deposited from which both males and females develop. These parasites oviposit in puparia, but never in larvae.

8. In 1916 and 1917 *N. brevicornis* and *D. cavus* were the chalcids most commonly found parasitising fly puparia.

9. The braconid, *A. manducator*, was bred very commonly each year from fly puparia collected in the autumn. In 1915 61 per cent. of the puparia were infected. In each year some of these parasites from the same batch of puparia

emerged in the spring and some in the autumn. The cause of this has not been ascertained, but it has been shown that the imagines from eggs laid by a single female appear at different times, even though the parasitised fly larvae are kept under identical conditions. These parasites attack large larvae. Virgin females readily attack larvae and lay numerous eggs from which males emerge. Only one parasite emerges from each infected puparium.

10. *A. cephalotes*, a smaller braconid, was bred frequently. It attacks small fly larvae. Several of the parasites emerge from each infected puparium.

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ON THE LIFE HISTORY OF *ASCARIS LUMBRICOIDES*, L.

PART IV[1].

By F. H. STEWART, D.Sc., Major I.M.S.

(With Plate XX.)

Ransom and Foster have published a preliminary account of experiments on the life history of *Ascaris lumbricoides* in the *Journal of Agricultural Research* of 19th November, 1917. They found that a repetition of my experiments on the feeding of rats and mice with ripe *Ascaris* eggs gave results agreeing very closely with those recorded by me in the *British Medical Journal* of July 1st, October 7th and December 2nd, 1916, and in *Parasitology* of February 1917.

In addition to these experiments, they made further attempts to infect pigs with *Ascaris suilla*, but with negative results.

Their experiments were conducted on pigs several months old, and they suggest that the failure of these, and of other experiments, may have been due to the animals employed being past the age of greatest susceptibility to infection.

In an experiment conducted by them in September, 1917, ripe eggs were administered to a pig two weeks old. This animal died seven days thereafter, and *Ascaris* larvae measuring from 0·7 to 1·2 mm. were found in the lungs, trachea and pharynx. This experiment agrees with those published by me in the *Indian Medical Gazette* of August, 1917, and in *Parasitology* of January, 1918. Ransom and Foster also found an *Ascaris* larva in a fragment of lung of a pig, which had died from unknown causes, in the intestine of which they also found numerous immature Ascarids, the largest about 50 mm. in length.

They state that guinea pigs are susceptible to infection with *Ascaris* larvae.

I have recently been able to perform three further experiments on young pigs[2], of which the following account may be given:

1 and 2. To each of two sucking pigs, aged four days, about 22,000 ripe eggs of *Ascaris suilla* were given. The eggs were 31 days old, and contained

[1] Part I, *Parasitology*, IX. p. 213; Part II, X. p. 189; Part III, X. p. 197.

[2] I wish to express my thanks to the following gentlemen who gave me the assistance required to carry out the above experiments: Dr Keatinge, Principal of the School of Medicine, Cairo, Mr Branch, Chief Veterinary Inspector to the Egyptian Ministry of the Interior, and Mr Casdagli.

active embryos. Doses of eggs from the same cultures were administered to three young white rats as a control on two successive days. The rats were killed on the 7th and 9th days after the first dose, when a considerable number of active *Ascaris* larvae were found in their lungs. On the 8th day after treatment both the sucking pigs showed signs of pneumonia. They were breathing at the rate of 140 per minute, and the temperature of one was raised half a degree above the normal.

1. The first sucking pig was killed on the 14th day. No *Ascaris* larvae were found in the trachea, or in a fragment of the lung. Numerous larvae were found, however, in the small intestine, caecum and rectum. Measurements as follows from specimens fresh in salt solution:

Small intestine	2·5, 2·72, 3·04, 3·20, 3·80 mm.
Caecum	2·96, 3·04 mm.
Rectum	2·4, 2·48, 2·9 mm.

2. The second sucking pig was killed on the 19th day after infection. The stomach, small intestine, caecum and colon were opened, the mucous membrane scraped and washed, and the washings sedimented and examined under a dissecting microscope. No larvae were found. The muscular and serous coats were not specially examined owing to lack of time.

3. A pig aged two months was found to be passing *Ascaris* eggs in the faeces. It was treated with Santonin, and four days thereafter its faeces did not contain eggs. When it was $2\frac{1}{2}$ months old about 50,000 ripe *Ascaris* eggs, one month old, were administered to it. Eggs from the same cultures were administered to three old white rats, which had previously been subjected to *Ascaris* infection. When these were killed, on the 7th day, one *Ascaris* larva only was found in their lungs. The pig was killed 31 days after infection. No worms were found in its intestine.

Anatomy of the larva of Ascaris suilla *from the intestine of the pig fourteen days after infection.*

The measurements of the total length of fresh specimens is given above. For the general outline see Pl. XX, fig. 1. The head (figs. 2 and 3) bears three lips with the four papillae characteristic of the adult. The internal surface of each lip is lined by thickened cuticle, and is grooved longitudinally (fig. 3). Each lip is furnished with a muscular bundle continuous with the muscular body of the oesophagus (fig. 2, *mus.*).

The cuticle of the body surface is marked by a series of rings 0·004 mm. in breadth (fig. 3). In sections stained with iron haematoxylin it is not darkly stained, and is therefore not markedly cuticularised. Each lateral line bears a lateral membrane extending nearly from the head to the tail, and supported by a firm triradiate cuticular skeleton (figs. 5 and 6), the basal plates of which are embedded somewhat deeply in the substance of the lateral lines.

The muscular system shows a distinct advance in development when compared with that of the larvae from the trachea of the mouse. The nerve

ring is prominent (fig. 7) lying slightly behind the junction of the anterior and middle third of the oesophagus. The excretory pore lies immediately behind the nerve ring. The nucleus of the excretory cell is a large and prominent body lying between the left lateral line and the oesophagus at the junction of the middle and posterior third of the latter organ (figs. 6 and 7).

The rudiment of the gonads is situated just behind the middle of the body length (fig. 8). It consists of two rudimentary tubes leading backward to a rudimentary external aperture in the ventral line. The outline of the tail is shown in fig. 9.

These larvae have therefore reached a more advanced stage than the specimens from the trachea. An ecdysis has doubtless occurred between the two stages.

Measurements of a specimen mounted in Canada balsam: total length 2·4 mm. Head to nerve ring 0·126 mm. Head to excretory pore 0·144 mm. Head to end of oesophagus 0·324 mm. Head to rudimentary sexual aperture 1·638 mm. Length of tail 0·0828 mm.

EXPLANATION OF PLATE XX.

Fig. 1. Outline of larva. ×80.
Fig. 2. The head. ×800.
Fig. 3. Transverse section through the lips, and oblique longitudinal section through the body wall at about the middle of the body length. ×800.
Fig. 4. Transverse section through the head immediately behind the lips. ×800.
Fig. 5. Transverse section immediately behind the nerve ring. ×800.
Fig. 6. Transverse section at the level of the nucleus of the excretory cell. ×800.
Fig. 7. The oesophageal region. ×320.
Fig. 8. The gonads. ×800.
Fig. 9. Outline of the tail. ×800.

Lettering: an., anus. *b.d.l.*, base of dorsal lip. *b.l.s.v.l.*, base of left subventral lip. *c.r.*, ring in cuticle of body surface. *D.*, dorsal. *d.l.*, dorsal line. *g.a.*, genital aperture. *go.*, gonad. *gr.*, groove on internal aspect of lip. *Int.*, intestine. *l.*, lip. *l.l.*, lateral line. *l.m.*, lateral membrane. *m.*, longitudinal muscular band. *mus.*, muscular bundle of lip. *n.e.c.*, nucleus of excretory cell. *n.r.*, nerve ring. *oes.*, oesophagus. *pap.*, papilla. *sk.*, skeletal support of lateral line. *V.*, ventral. *v.l.*, ventral line.

THE INCUBATION PERIOD OF THE EGGS OF *HAEMATOPINUS ASINI.*

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and L. LINZELL,

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INTRODUCTION.

Three kinds of lice are found on horses, two belonging to the Mallophaga or scale-eating lice and one to the Siphunculata or blood-sucking lice.

Of these, one, *Trichodectes equi*, is not very commonly found; whilst the other two, *T. pilosus* and *Haematopinus asini*, have both been common on the horses and mules of the Home Forces during the war. *T. pilosus* was found in about 10 per cent. of the total cases, usually as a mixed infestation, and chiefly in remounts from America or other places abroad, where the transport entailed a long sea voyage.

Of the two latter kinds *H. asini* is the more important because:

(*a*) It occurs more frequently.

(*b*) The irritation produced by it is greater.

(*c*) Constitutional disturbances are set up in grossly infested cases to such an extent that a loss of condition progressing eventually to absolute emaciation is produced.

(*d*) The possibility exists of this insect acting, like so many other blood-sucking parasites, as a carrier of disease, although hitherto no disease of horses has been definitely traced to it.

(*e*) Lastly, it offers far greater obstacles to lasting eradication than do either *T. equi* or *T. pilosus*, and one of the most annoying features of infestation by this parasite is the tendency of apparently cured animals to become reinfested after the lapse of a few weeks.

In view of the foregoing considerations, experiments were conducted only on the eggs of *H. asini*, and the following remarks apply only to that species.

Most of the dressings in common use in veterinary practice for the treatment of lousiness in horses will, if carefully applied, suffice to kill all living parasites, although the latter are capable of surviving treatment with many *supposed* lethal substances, and in particular seem to enjoy a truly remarkable immunity to arsenic, mild doses of which exert only a stupefying effect. The nits or eggs, however, are extremely resistant, and no dressing at present in use can be relied on to devitalise these with certainty, even the most efficient agent tested allowing 2 per cent. to hatch after five minutes complete immersion.

The experiments herein detailed were undertaken to determine the incubation period of the eggs. It was hoped by this means to fix some definite period, during which dressings are necessary to prevent these apparent reinfestations which, as subsequently confirmed, may not infrequently be due to the late hatching out of eggs.

PRELIMINARY TRIAL.

In order to ascertain if the nits of *H. asini* could be incubated successfully when removed from the horse, some nits were collected on 20. IV. 1918, at No. 1 Reserve Veterinary Hospital, Woolwich. The nits, 79 of which appeared sound, were placed in a tube and carried away in a vest pocket (at ca. 75°–80° F.). Subsequently they were left in a discarded coat for 24 hours at ca. 55°–60° F., before being placed in a small entomological box suspended from a man's neck in a thin cotton bag between the skin and shirt. The temperature in this situation when indoors ranged between ca. 90° F. by day, and ca. 95° F. at night; when out of doors the temperature fell to a variable extent. On the fourth day, through an oversight, the bag with the nits was left for 10–11 hours at ca. 63° F., but afterwards it remained next the skin except when removed for examination.

The age of the eggs was of course not known. They hatched as follows:

Record relating to 79 *eggs incubated on man.*

On day ...	...	2	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
There hatched ...	1	3	5	5	2	3	7	4	1	1	2	2	4	–	2	–	1	1	eggs.

Total hatched ... 46 (58 %).

EXPERIMENTS WITH DATED EGGS.

(*a*) *Collection of Eggs.* Attempts were made in various ways to obtain eggs within 24 hours of their being laid. Cages composed of felt rings with gauze tops failed because the horses usually succeeded in moving the pads by twitching their skin, and, when this difficulty was overcome, it was found that the lice persistently forced their way out underneath the felt. Various types of cage were tried with both tops and bottoms of gauze, but these failed, owing to the temperature inside the box being too low for oviposition.

Attempts to feed the female lice on animals other than the horse were likewise unsuccessful[1].

Eventually cages were made by covering the bottom of pill boxes (ca. $1\frac{1}{2}$ inches diameter) with gauze and the top with linen; these boxes were filled loosely with horse-hair and placed under a felt pad (ca. 9 inches × 3 inches × $\frac{3}{4}$ inch). Three holes, to fit the boxes, were cut in the centre of the felt to a little less than the depth of the box and in the centre of each of these depressions a hole ($\frac{1}{4}$ inch) was cut to ensure ventilation. The pad with its three cages was fastened to the horse's side by a kind of broad surcingle made of open mesh ($\frac{1}{2}$ inch) string netting. About 50 ♀♀ and 12 ♂♂ were placed in each box. This device answered our purpose, but many lice failed to feed through the gauze and consequently the number of eggs obtained was limited.

(*b*) *Incubation at* 100° *F.* (*dry*). The first trials were made by simply placing the eggs in an incubator at 100° F. Of ten batches of about a dozen each, not a single egg hatched in a month, none showed signs of development —they had simply dried up.

To prevent this dessication the boxes were placed on a wire tray supported over water so as to keep the atmosphere always saturated with moisture. Under these conditions a batch of ten eggs all hatched on the sixteenth day.

(*c*) *Incubation at* 70°–80° *and* 100° *F.* (*damp*). The next trial was made at a lower temperature in an old incubator with a fluctuating temperature of from 70° F. at night to 80° F. by day. The eggs were collected every 24 hours and each batch divided into two equal lots, the first lot being placed in the above incubator with a dish of water, and the second incubated simultaneously at 100° F.

The following is the result.

	70°–80° F.	100° F.	
Eggs hatched on day 15 (evening) ...	—	14	Total hatched 112
,, ,, 16	—	91	
,, ,, 17 (morning) ...	—	7	
Eggs failed to hatch (2 months) ...	117	2	Total failed 119

Of the eggs incubated at 70°–80° F. 94 developed moulds, 12 became discoloured and soft, and 11, which after three months showed no change, were found on being opened to contain a viscid opalescent fluid.

(*d*) *Incubation at* 85°–100° *and* 100° *F.* Two experiments were made, each in a humid atmosphere and with a temperature fluctuating between 85° F. and 100° F. The first was made in the incubator mentioned in the last experiment, 36 eggs in five lots being used, and five lots of two eggs each as controls. The second was made by placing the eggs in a bag and incubating by a similar method to that used in the preliminary experiment, 58 eggs in

[1] Of seven lice kept on the arm of one of the writers, only two bit and succeeded in filling themselves with blood, but they died next day whilst the remainder lived three days longer. Out of some dozens of lice tested at various times, only three have been induced to feed.

six lots being used, again with two eggs as control for each lot. The results in both cases were similar and the table below shows the net result.

	85°–100° F.	Control 100° F.
No. of batches	11	11
Eggs hatched on day 16 ...	—	17
,, ,, 17 ...	3	5
,, ,, 18 ...	16	—
,, ,, 19 ...	11	—
,, ,, 20 ...	8	—
,, ,, 21 ...	5	—
,, ,, 22 ...	7	—
,, ,, 23 ...	—	—
,, ,, 24 ...	3	—
,, ,, 25 ...	1	—
,, ,, 26 ...	7	—
,, ,, 27 ...	2	—
,, ,, 28 ...	1	—
,, ,, 29 ...	3	—
,, ,, 30 ...	—	—
,, ,, 31 ...	—	—
,, ,, 32 ...	2	—
,, ,, 33 ...	3	—
,, ,, 34 ...	1	—
Failed to hatch (2 months) ...	21	—
Total	94	22

(*e*) *Incubation on the Horse.* A final test was made with two batches of five and four eggs respectively, actually laid and remaining in a horse's coat. These were obtained in July, 1918, in one of the felt-ring cages mentioned under *Collection of Eggs.*

No. of batches	2
Eggs hatched on day 17	3
,, ,, 18	3
,, ,, 25	1
Eggs lost	2
Total number of eggs ...	9

CONCLUSIONS.

1. Our experiments show that the eggs of *H. asini* may take as long as a month or more to hatch. Therefore animals infected with *H. asini* must be kept under observation, and the last dressing given not less than 34 days after the time the treatment started.

It has not been possible to determine the minimum time required for a horse-louse to develop from the egg to the fertile female, but from analogy it will probably be about a fortnight, it having been found that in insects of this class the incubation and maturation periods are approximately equal.

This, if correct, would mean that supposing all active stages are killed at each dressing and the treatment repeated at ten-day intervals, four dressings at least must be given, for, although no more eggs will be laid during the period over which the dressings extend, there is every probability that if this period is curtailed a few of the original stock may hatch after a month and restart the infestation.

2. The normal incubation period would appear to be 16–20 days, and the minimum period, under natural conditions, about 15–16 days.

3. A very small amount of *dry* heat will kill eggs. Even at blood heat it was found that 24 hours in a dry atmosphere prevented hatching.

It is evidently due to the effect of temperature that the lice in hot weather migrate to sheltered parts of the body. The eggs are usually laid close to the skin, and, in a partly clipped horse, the lice migrate to the unclipped portions.

4. Moist cold kills the eggs, whereas dry cold only has the effect of lengthening the incubation period by a few days. How long they can withstand this dry cold has not yet been determined, but a week in a cold *dry* room with a temperature of about 50° F. resulted in killing about 50 per cent. and lengthening the incubation period of the remainder from the normal 16 days at 100° F. to 18 days.

ERRATUM TO VOL. XI.

p. 225, line 12, *read* 0·5 (caustic soda 0·5 pt.) *for* 5

OBSERVATIONS ON THE BIOLOGY OF THE IXODIDAE.

PART III. DEALING WITH THE BEHAVIOUR OF THE SEXES IN *AMBLYOMMA HEBRAEUM*, *HYALOMMA AEGYPTIUM* AND *RHIPICEPHALUS BURSA* WHEN UPON THE HOST.

By GEORGE H. F. NUTTALL, F.R.S.

The experiments herein recorded were conducted with a view to supplementing the biological studies on ticks previously published by me in *Parasitology*, Vols. VI and VII, and, more particularly, to acquire a knowledge of the behaviour of the sexes upon the host. For this purpose, ticks belonging to three different genera were employed, *i.e. Amblyomma*, *Hyalomma* and *Rhipicephalus*, since their behaviour was likely to differ more widely than in members of one genus, although some members of the recognised genera, as I am perfectly aware, may differ still more widely in their habits than do the species to which this communication relates.

METHODS.

The adult ticks were placed upon a ram's scrotum enclosed in a canvas bag of suitable size which could be tightened at the neck by drawstrings running in opposite directions through a seam at the top of the bag. Furthermore the latter was secured by two cords that ran belt-wise around the animal. That the behaviour of the ticks in this confined area is practically the same as when they are permitted to roam at will upon the host was amply proved in my earlier experiments.

The ticks were given identification marks by painting a part of their backs with various colours. The paints, consisting of different kinds of sealing wax dissolved in alcohol, were applied to the ticks by means of a sharply pointed match. The alcohol evaporated soon after the paint was applied, and the hard glossy crust of wax that was formed in no way affected the ticks adversely. The colours had to be reapplied from time to time and no confusion of individuals resulted by the use of the method, except in some cases with *R. bursa* males, to whose smooth glossy backs the wax adhered badly.

Coloured lines were drawn with greased pencil upon the surface of the scrotum, front and back, whereby it was divided into areas which facilitated

the recording of the ticks' wanderings from one seat of attachment to another. A record was mapped upon a daily chart, the signs ♂ and ♀, pointing in different directions and variously coloured, denoting the exact position of individual ticks on successive days. The distances traversed by the ticks in their wanderings were mostly recorded approximately.

I. AMBLYOMMA HEBRAEUM.

The general biology of this species has already been described by me (1915, *Parasitology*, VI. pp. 409–419), it being stated (*Ibid.* p. 414) that Lounsbury is the only author who refers to the behaviour of the sexes upon the host. The observations here recorded amplify those of Lounsbury, which are but cursorily treated by this author.

The adults (Lot N. 1732) used in the following experiments belonged to the same strain that was employed in my earlier studies (*loc. cit.*). They had emerged on 9. xii. 1913. There were 167 ♂♂ and 95 ♀♀ alive on 25. i. 1915, *i.e.* after having been kept unfed at room temperature for 412 days. A number of these ticks were placed successively on a ram's scrotum as follows:

	Day recorded in protocol	♂	♀
On 25. i. 1915	1	12	—
	4	—	13
	10	—	5
	12	—	2
	16	2	—
	23	—	4
	39	—	6
	Totals	14	30

Of these ticks, one ♂ (No. 12) was lost after three days and two ♀♀ (Nos. 29, 30) disappeared. The following record relates therefore to 13 ♂♂ and 28 ♀♀, and their behaviour upon the host on successive days:

Records relating to *A. hebraeum* Males Nos. 1–14.

♂ 1. Days 1–10 fixed*; on 11th joined by ♀ 8 which dropped† on 20th, the ♂ continuing fixed; on 36th he rotates 45°; on 37th he appears excited; on 39th he shifts ca. 2 mm. from his original seat of attachment (a distinct crater); he is excited on 42nd, 47th; removed on 132nd day.

♂ 2. Days 1–10 fixed; on 11th joined by ♀ 12 which dropped on 20th; he is approached on 20th by ♀ 18; on 21st he is joined by ♀ 18 which dropped on 29th; he is excited on days 29, 30, 33, 36, 37; ♀ 23 is put to him on 39th and stays with him till she dropped on 50th; he is excited on days 50, 54, 57; remains fixed to 141st day.

* The term "fixed" denotes that the tick remained attached immovably at one spot.

† Meaning dropped off the host in an engorged condition.

♂ 3. Days 1–11 fixed; on 11th put to him ♀ 7, but she did not stay; on 12th ♀ 9 joined him and dropped 21st; on 23rd put to him ♀ 19 which dropped on 31st; he continues fixed, appearing excited on days 35–37; on 39th put to him ♀ 24 which dropped 50th; he is excited on days 50, 54; on 57th he shifts a few mm. and thereafter remains fixed to 141st day.

♂ 4. Days 1–12 fixed; on 12th put to him ♀ 13 which dropped on 22nd; on 23rd put to him ♀ 20 which dropped on 33rd; he is excited on days 35–37, 39; on 39th put to him ♀ 25 which dropped on 48th; he is excited on days 51, 54, 57, but remains fixed to 141st day.

♂ 5. Days 1–12 fixed; on 12th put to him ♀ 7 which dropped on 21st; he is excited on 23rd when ♀ 29 is put to him but she disappeared 24th; on 23rd he shifts ca. 1 cm. and is excited on days 32, 38, 50; on 57th he shifts 3 mm.; he is removed 77th day to illustrate his changed coloration.

♂ 6. Days 1–5 fixed; on 6th shifts slightly; on 12th put to him ♀ 14 which dropped 22nd; on 30th put to him ♀ 22 which dropped 32nd; he is excited on days 33, 35, 38; on 39th put to him ♀ 30, she was lost on 40th; he is excited on days 50, 51; on 54th he shifts 6 mm. and then remains fixed to 141st day.

♂ 7. Days 1–11 fixed; on 11th put to him ♀ 11; on 31st he is found loose and wandering 4 cm. away, he is seized and put to ♀ 11 with which he copulates and stays till she dropped on 37th when he wanders to posterior surface of scrotum and anchors close to males 10 and 12; on 38th he is excited; on 49th he shifts slightly; on 50th he wanders freely and on 51st is found dead.

♂ 8. Days 1–6 fixed; on 6th find ♀ 1 alongside, she dropped 22nd; on 23rd he is excited and put to him ♀ 21 which dropped on 32nd; he is alone and excited on days 32, 35–38; on 39th put to him ♀ 26; the pair shifts together on 40th about 1 cm. and female is seen to drop on 49th; on 50th he is excited; on 57th he shifts 8 mm. and remains fixed thereafter until removed on 132nd day.

♂ 9. Days 1–6 fixed; on 8th ♀ 5 approaches to within 5 mm. of him and stays there till 10th; on 11th copula, the pair having shifted together ca. 1 cm.; on 12th the pair in copula; female dropped on 18th; he is much excited on days 18, 19; on 20th ♀ 15 pairs with him, she dropped 29th; he is excited on days 31–33, 37, 38, 40, 44–46, 50–54, 56–58, 60, 77; on 52nd he shifts 7 mm. but remains fixed thereafter until removed on 132nd day.

♂ 10. Days 1–9 fixed; on 9th find ♀ 6 venter to venter with him, she becomes fully engorged but on 25th he leaves her and reattaches himself 5 mm. away, she dropped on 26th; on 29th he shifts 13 mm. to push away ♂ 11 and join ♀ 16 then ¼ gorged; this female is torn loose accidentally on 31st; he is excited on days 31, 33, 36–38, 45; on 49th ♀ 28 is found to have come a distance of 3 cm. to join him, he having shifted his anchorage 5 mm., the pair in copula. On 52nd he is excited, alongside the same female, the latter dropped on 56th; he is excited on days 56, 58; on 99th he shifts ca. 5 mm., and thereafter remains fixed till removed on 132nd day.

♂ 11. Days 1–10 fixed; on 11th find ♀ 10 alongside him, she dropped 20th; on 21st he is still fixed; on 22nd he is joined by ♀ 16, copula seen; on 29th, whilst the female is ¼ gorged, he is crowded away by ♂ 10, the female being accidentally torn off on 31st; he is excited on days 30–31, 33, 36–7, 45–6, 52, 54, 56–58, 77, but remains fixed till removed on 132nd day.

♂ 12. Days 1–3 fixed, afterwards lost.

♂ 13. Put to ♀ 4 on day 16; on 19th he shifts 3 mm. away from female, but on 21st is found close to her again, she dropped 35th; he is excited on days 40–45, 50, 52, 54, he shifts 5 mm. on 57th, is excited on 58th and shifts slightly on 99th, after which he remains fixed till removed on 132nd day.

♂ 14. Put to ♀ 2 on day 16, she dropped 22nd and he shifts 5 cm.; on 28th he shifts 15 mm.; he is excited on days 29, 37; on 40th he is joined by ♀ 27 which dropped on 49th; he remains fixed, is excited on days 52, 54, 56, but does not change anchorage till removed on 132nd day.

Records relating to *A. hebraeum* Females Nos. 1–28.

	Day when put on ram	Day on which ♀ was sought or put to ♂	Feeding of ♀ on successive days b. = began to feed f. = fully gorged g. = gorged	♀ dropped off ram on day	♀ ceased ovipositing on day	Eggs began to hatch on day	Remarks (h. = hatched)
♀ 1	4	6 sought ♂ 8	9 b., 18 ⅓-g., 19 ½-g., 20–21 f.	22	—	—	few eggs, none h.
♀ 2	4	16 put ♂ 14 to her	18 ⅓-g.	22	78	102	normal number eggs
♀ 3	4	failed	—	9 lost	—	—	—
♀ 4	4	16 put ♂ 13 to her	30 b., 31 ¼-g.	35	—	—	no eggs laid, ♀ alone at first, approached by ♂ 13
♀ 5	4	11 sought ♂ 9	—	18	77	102	approached ♂ on days 8–10; few eggs h.
♀ 6	4	9 sought ♂ 10	20 ¼-g., 23 f.	26	96	104	left by ♂ on 25th; few eggs h.
♀ 7	4	11 put to ♂ 3 but left; 12 put to ♂ 5	16 b., 19 ¼-g., 20 ⅓-g.	21	91	103	normal number eggs; ♀ got loose but was replaced
♀ 8	4	11 sought ♂ 1	18 ⅓-g., 19 f.	20	—	—	died, laid no eggs
♀ 9	4	12 sought ♂ 3	16 b., 18 ⅓-g., 19 ½-g., 20 f.	21	83	89	normal number eggs
♀ 10	4	11 sought ♂ 11	20 ¼-g.	21	80	108	few eggs h.
♀ 11	11	11 put to ♂ 7	18 b., 28 ⅛-g., 33 ½-g.	37	—	—	fed v. slowly alone, ♂ 7 put to her 31st, copulated; she died without laying
♀ 12	4	11 sought ♂ 2	18 f.	20	—	—	few eggs, none h.
♀ 13	12	12 put to ♂ 4	16 b., 19 ¼-g., 21 ⅓-g.	22	83	103	normal number eggs
♀ 14	12	12 put to ♂ 6	19 ⅓-g.	22	95	103	few eggs h.
♀ 15	10	20 sought ♂ 9	23 b., 26 ¼-g., 28 f.	29	—	—	*
♀ 16	10	22 sought ♂ 11; 29 sought ♂ 10	26 ¼-g.	31	85	110	normal number eggs laid though torn loose accidentally
♀ 17	12	failed	—	—	—	—	torn off 23rd, died 99th, laid few eggs
♀ 18	19	20 approached and 22 sought ♂ 2	24 ¼-g., 25 f.	29	—	—	few eggs laid, none h.
♀ 19	23	23 put to ♂ 3	28 ⅛-g., 29 ⅓-g., 30 f.	31	106	121	few eggs h.
♀ 20	23	23 put to ♂ 4	28 ⅛-g., 29 ⅓-g., 30 ⅓-g., 31–2 f.	33	—	—	*
♀ 21	23	23 put to ♂ 8	28 ⅛-g., 29 ⅓-g., 30 ½-g., 31 f.	32	—	120	few eggs laid, few h.
♀ 22	23	23 put to ♂ 6	28 ⅛-g., 29 ⅓-g., 30 ⅓-g., 31 f.	32	108	123	normal number eggs
♀ 23	39	39 put to ♂ 2	45 ¼-g., 47 ½-g.	50	—	—	few eggs laid, none h.
♀ 24	39	39 put to ♂ 3	45 ¼-g., 47 ½-g.	50	—	—	*
♀ 25	39	39 put to ♂ 4	45 ¼-g., 46 ¼-g., 47 ½-g.	48	—	—	*
♀ 26	39	39 put to ♂ 8	45 ¼-g., 46 ¼-g., 47 ½-g.	49	—	—	no eggs h.
♀ 27	39	40 sought ♂ 14	45 b.	49	—	131	few eggs h.
♀ 28	39	49 sought ♂ 10	54 ⅓-g., 56 f.	56	—	—	she came 3 cm. from anchorage to find ♂

Note. Copulation was observed to take place in the case of ♀ 5 on days 11 and 12, ♀ 11 on day 31, ♀ 16 on day 22, ♀ 28 on day 49. * The ♀ was not allowed to oviposit.

The foregoing protocols demonstrate the following regarding *A. hebraeum*:

Males. Of 13 ♂♂ one died on the 51st day, one was removed and figured on the 77th day, six were lively when removed on the 132nd day, one was lost on the 136th day, and four were lively when removed on the 141st day.

The males with few exceptions do not move or scarcely move from their seat of attachment upon the host. Thus ♂ 1 shifted ca. 2 mm. on day 39 and remained fixed till day 132; ♂ 2 and ♂ 4 remained on one spot for 141 days; ♂ 3 shifted a few mm. on the 57th after which he remained fixed till day 141; ♂ 5 shifted 1 cm. on the 23rd, 3 mm. on the 37th, he was removed on the 77th; ♂ 6 shifted slightly on the 6th, 6 mm. the 54th, afterwards remaining fixed to the 141st; ♂ 7 wandered around the scrotum on the 37th, shifted slightly on the 49th, wandered on the 50th and was dead on the 51st; ♂ 8 shifted 1 cm. with his female on the 11th, and 8 mm. on the 57th, and remained fixed afterwards until the 132nd ; ♂ 9 shifted 1 cm. with his female on the 11th, 7 mm. the 51st; ♂ 10 shifted 5 mm. on the 25th, 13 mm. on the 29th, 5 mm. on the 49th and again on the 99th, remaining fixed till the 132nd; ♂ 11 was slightly displaced by a male on the 29th, then remained fixed till the 132nd; ♂ 13 shifted 3 mm. on the 19th, 3 mm. on the 21st, 5 mm. on the 57th, slightly on the 99th afterwards remaining on one spot to the 132nd; ♂ 14 shifted 5 cm. on the 22nd, but remained fixed afterwards to the 132nd day. On two occasions males shifted in company with their females.

Males readily attach themselves in the absence of females. The males are sought by the females. When ready for copulation the males extend their legs and erect their bodies so as to seize and hold a passing female. Males frequently exhibit this sexual excitement when the skin of the host is touched or moved, no female being in the vicinity. Such males are described as "excited" in the protocols. In many instances virgin females were put to such expectant males who promptly seized them, the females subsequently anchoring themselves on the same spot with the males.

The act of copulation was observed on five occasions, it occurs as I have described elsewhere for *Ornithodorus* and *Ixodes*[1]. A male may pair with several females, a fact recorded by L. and J. Roberts (see Nuttall, p. 414). My records show that ♂ 3 paired with four females, ♂ 2, ♂ 4, ♂ 6 and ♂ 10 with three females each, etc. ♂ 3 fertilized three females, ♂ 6, ♂ 10 and ♂ 11 fertilized two females each, whilst ♂ 2 failed to fertilize three females.

Males remain upon the host long after the females have dropped off gorged. Whilst they remain for days without changing their orientation, they may rotate slightly (10–45°) about the seat of the puncture in which their mouthparts are fixed.

The colour of the males undergoes a remarkable change as the result of a prolonged stay upon the host, the colour change was very distinct by the 77th day, still more so on the 131–141st day. The colour changes observed will be described in a further communication.

[1] Nuttall and Merriman, 1911, *Parasitology*, IV. pp. 39–44, 1 fig.; Nuttall, *Ibid.* VI. p. 81

Females. Of 28 ♀♀ under observation, one was lost, one was torn loose by accident, and 26 became engorged. Of these four were killed and preserved, leaving 22 of which six yielded normal progenies, seven yielded eggs few of which hatched, five laid eggs that did not hatch, whilst four died without ovipositing.

That females will not as a rule attach themselves in the absence of males was observed by Lounsbury (see Nuttall, p. 414). The females settle down to feed near males, and usually after 2–8 or more days, they wander about, as I have found, in search of anchored males which seize them as they approach. Females may seek two males in succession, but one male usually suffices. Females feed slowly in the absence of males. The rate at which females become engorged varies even when they are paired. From the time when they show the first naked eye signs of feeding, it usually takes 4–5–6 days before they drop off fully gorged, but this period may be prolonged to 19 or more days[1]. The female swells gradually so that she appears successively "$\frac{1}{5}$," "$\frac{1}{4}$" or "$\frac{1}{2}$-gorged" (as recorded in the protocols), whereas the fully gorged condition is reached rapidly. A female may imbibe as much blood in a few hours, prior to dropping off, as during several previous days. She usually drops off promptly when fully gorged, but there may be a delay of 24 hours or so possibly owing to difficulty in releasing her mouthparts.

II. HYALOMMA AEGYPTIUM.

The general biology of this species has been considered in previous papers (1915–16, *Parasitology*, VI. pp. 105–110; VII. p. 436).

The adults (Lot N. 1305) used in the following experiments belonged to the same strain used in my earlier observations (*loc. cit.*). They were fed upon a hedgehog as nymphs, and emerged as adults on 3–6. vii. 1914. There were some hundreds alive after being kept unfed at room temperature for 208 days. A number of these ticks were placed upon the ram's scrotum as follows:

	Day recorded in protocol	♂	♀
On 27. i. 1915	1	8	8 (♀ 6 was lost)
	17	—	1 (♀ 9 to replace ♀ 6)

The following record relates therefore to 8 ♂♂ and 8 ♀♀ and their behaviour upon the host on successive days:

Records relating to *H. aegyptium* Males Nos. 1–8.

♂ 1. Days 1–122 fixed, *i.e.* the male never moved from his first point of attachment in the right inguinal space outside the bag. Only one female escaped from the bag during the experiment, attaching herself in the opposite inguinal space.

♂ 2. Days 1–29 fixed, though a ♀ attached herself close by; between 30th and 133rd day he altered his anchorage slightly on three occasions, moving 11, 4, and 4 mm. respectively.

[1] Lounsbury (Nuttall, p. 418) saw females remain as long as 25 days attached to the legs and feet of goats. He attributes these differences to the varying blood supply obtained by the tick in different situations upon the host.

♂ 3. Days 1–7 fixed; on the 8th he had shifted 5 cm. to join ♀ 5 with which he was seen to copulate on the 11th; she dropped on the 13th and he stayed fixed on the same spot until day 64 when he was removed.

♂ 4. Days 1–5 fixed; on 6th had shifted 4 cm. to join ♀ 7 which dropped on 12th whilst he remained fixed until 13th; on 14th he shifted 10 cm. to back of scrotum joining ♀ 3 which he abandoned on 20th, anchoring himself 12 mm. away where he remained fixed till 30th when he shifted 13 cm. to front of scrotum; he subsequently anchored himself on seven different spots within a circle of 3·5 cm. diameter, after having moved 18 mm. on 33rd, 22 mm. on 35th, 11 mm. on 45th, 24 mm. on 54th, 1 cm. on 56th, 6 mm. on 120th, 2 cm. on 139th day.

♂ 5. Days 1–5 fixed; on 6th had shifted 4 cm. to join ♀ 2 which he abandoned on 13th, being found anchored in front of scrotum 8 cm. away. He remained fixed and alone, shifted 10 cm. to back of scrotum on 17th and remained fixed till 22nd when he was found wandering and excited; he was now put to anchored ♀ 9 which he fertilized. This female dropped on 27th but he stayed fixed till 36th when he shifted 15 mm., after which he shifted 4, 10, 14, 8 and 5 mm. respectively according to records made on days 48, 51, 110, 121, 139.

♂ 6. Days 1–4 fixed; on 6th had shifted 3·5 cm. to join ♀ 8; on 11th copulated and on 13th abandoned her, shifting 9 cm. to front of scrotum; ♂ lost on 14th.

♂ 7. Days 1–10 fixed; on 11th had shifted 3·5 cm. to join ♀ 4 (copula); on 13th had abandoned her and shifted 16 cm. to front of scrotum; on 19th he had shifted 13 mm., after which he shifted four times within a small area, *i.e.* 6, 3, 4 and 5 mm. respectively on days 41, 47, 56, 64, remaining afterwards fixed till 139th day.

♂ 8. Days 1–14 fixed; on 15th shifted 7 mm., on 21st shifted 10 mm. to near a ♀ with her male; on 23rd shifted 9 mm., on 24th shifted 5 cm. to front of scrotum, on 27th shifted 11 mm., and on 29th 5 cm. to back of scrotum; thereafter, always alone, he shifted nine times within a small area, *i.e.* 11, 10, 5, 12, 14, 5, 12, 11 and 10 mm. respectively on days 36, 38, 47, 52, 56, 61, 97, 121, 123, remaining fixed thereafter till 139th day.

Records relating to *H. aegyptium* Females Nos. 1–9.

	Female dropped from host on day	Female ceased laying on day	Eggs began to hatch on day
♀ 1. Days 1–10 fixed, alone; on 10th nearly gorged, on 12th gorged. No ♂ was seen to approach but she was fertilized	18	65	56
♀ 2. Days 1–5 fixed, alone; on 6th approached by ♂ 5; on 7th gorged; on 10th copula; on 13th the ♂ gone	14	57	50
♀ 3. Days 1–4 fixed, alone; on 11th slightly gorged; on 14th joined by ♂ 4, copulates and begins to feed; on 20th ♂ gone	21	85	71
♀ 4. Days 1–10 fixed, alone; on 11th she joins ♂ 7 and copulates; on 13th ♂ gone; on 18th she is fully gorged	19	90	70
♀ 5. Days 1–7 fixed, alone; on 8th joined by ♂ 3; on 10th she is ¼-gorged and on 11th copulates	13	61	51
♀ 6. Lost			
♀ 7. Days 1–5 fixed, alone; on 6th joined by ♂ 4; on 9th she is ¼-gorged and copulates on 10th	12	64	58
♀ 8. Days 1–2 fixed, alone, but near ♂ 5; on 3–5th alone; on 6th joined by ♂ 6; on 11th copulates; on 13th ♂ gone and she is partly gorged; on 15th she is fully gorged	17	57	50
♀ 9. Put on ram on day 17 near ♂ 5; on 20th alone; on 22nd put excited wandering ♂ 5 to her; he stayed with her until she dropped and did not shift for days after. She dropped 27th (10th day after being put on ram)	27 (10)	85 (68)	73 (56)

The foregoing protocols demonstrate the following regarding *H. aegyptium*:

Males. ♂ 1 remained isolated from females outside the bag and did not shift his position during 122 days. ♂ 2 remained fixed for 29 days and shifted three times afterwards between 30th and 133rd days. ♂♂ 3–8 remained fixed for 7, 5, 5, 4, 10, and 14 days respectively before they sought females; ♂ 6 was lost in his wanderings.

After a period of quiescence during which they indulged in a preliminary feed, the shifting about of the males was very pronounced as long as females were present. After the females had dropped off gorged, the males remained anchored within a very restricted area, shifting usually but a few mm. at a time up to the 139th day, except in the case of ♂ 6 which was lost after the 14th, and ♂ 3 which was removed on the 64th day.

♂ 5 sought two ♀♀, the rest sought but one ♀, but without doubt the males would have each sought several females had opportunity offered. The male may stay but a short time with a female or he may remain several days with her. After the female with which a male has mated abandons the host, the male may either wander away or remain attached for days or indefinitely at the same anchorage he occupied when the female was present. Females brought close to anchored males caused them to become greatly excited; a female (♀ 5) placed in the vicinity of a male, anchored herself beside him.

Females. With but one exception the females did not shift their anchorage from start to finish; they were all sought by males, with the possible exception of ♀ 4, whilst, as previously stated, ♀ 5 was placed near an excited male. The male that fertilized ♀ 1 remained with her so short a time that the union escaped observation. The females did not appear to copulate with more than one male. ♀♀ 2–9 dropped from the host 8, 7, 8, 5, 6, 6 days respectively after being approached by a male or having been seen to copulate. All of the females were fertilized and yielded a normal number of offspring.

III. RHIPICEPHALUS BURSA.

For an account of the general biology of this species, the reader is referred to my earlier papers (1913–15, *Parasitology*, VI. pp. 139–140; VII. pp. 438–448, 457–460).

The adults (Lot N. 1305*a*) used in the following experiments belonged to the same strain that was employed in my previous studies (*loc. cit.*). They had emerged 9. iii. 1914. On 26. i. 1915 there were some hundreds alive after having been kept unfed at room temperature for 323 days. The ticks were placed on the ram's scrotum in successive batches as follows:

	Day recorded in protocol	♂	♀
On 26. i. 1915	1	11	11
	16	—	3
	18	—	3
	Totals	11	17

All of the 17 ♀♀ were fertilized and had plentiful offspring. Of the ♂♂, 1 anchored outside the bag and was lost on the 39th day, 1 died on 84th day, 3 were lost on the 98th, 111th, and 122nd days respectively, leaving 6 that were removed in a lively condition on the 140th day, having paired with further females that had been added on the 128th day and which dropped off on the 137–140th day.

Owing to the glossy backs of the males, a few did not retain their marks, some confusion arose whereby the records were partly vitiated. A sufficiently accurate record could be kept, however, to form an idea regarding their general behaviour.

Records relating to *R. bursa* Males 1–11.

♂ 1. Days 1–3 fixed; on 4th wandered; on 7th found with ♀ 5 with which he stayed till she dropped on the 9th and the ♂ was seen to walk away; on 11th approached ♀ 9; on 12–16th alone and fixed; on 17–21st alone, having shifted around scrotum; on 22nd had wandered round scrotum to join ♀ 16 with which he stayed till she dropped on 29th; on 30th he had shifted slightly, remaining alone till 36th having shifted on 32nd; on 36th a semi-gorged female (♀ 17) was placed beside him, they remained near each other till she dropped on 41st; on 42nd he had shifted, on 43rd he wandered round the scrotum and on 44–46th retraced his steps: on 48th shifted slightly and again on 52nd; he remained almost stationary till 60th, shifted round scrotum on 62nd, remained fixed till 84th when recording ceased.

♂ 2. Days 1–4 fixed; on 5th has joined ♀ 5; on 7th shifted 3 mm. to ♀ 4 which dropped on 10th when he shifts downward to near ♀ 9 which dropped on 13th; on 14th he approaches ♀ 11 which dropped 16th; on 17–20th he was alone having wandered round the scrotum; on 21st he shifted slightly and again 22nd; on 34th he wandered round the scrotum, upward on 37th, downward on 38th, round scrotum on 39th, and shifted about further on days 43, 46, 55, 58, remaining fixed till the 62nd day when he had wandered and could no longer be identified.

♂ 3. Days 1–5 fixed; on 7th near ♂ 2 and ♀ 4 both of which were gone on 12th; on 14th he was near ♀ 11 with other males, she dropped 16th but he stayed on near the males till 19th when he shifted round the scrotum after which he could not be identified.

The records of the other males are essentially similar and they need not be dwelt on. Suffice it to say that

♂ 4. Sought ♀ 4 on the 4th, ♀ 11 on the 5th, ♀ 8 on the 7th, ♀ 2 on the 12th, approached ♀ 14 on the 18th, and ♀ 13 on the 19th; he was only seen to copulate with ♀ 11 and ♀ 13.

♂ 5. Sought ♀ 8, ♀ 6, ♀ 11, ♀ 12, and ♀ 14; he certainly copulated with ♀ 6.

♂♂ 6–11. These merely afforded similar records to the foregoing but none of the males sought so many females and two of the males lost their markings at an early date.

Records relating to *R. bursa* Females 1–17.

	Female dropped from host on day	Female ceased laying on day	Eggs began to hatch on day
♀ 1. Days 1–5 alone, fixed; on 7–9th joined by ♂ 8	9	40	46
♀ 2. Days 1–7 alone, fixed; on 10th sought by ♂ 4. Fully gorged on 11th	14	45	46
♀ 3. Days 1–3 alone, fixed; on 4th found with ♂ 4. ½-gorged on 10th	12	43	46
♀ 4. Days 1–4 alone, fixed; on 7th joined by ♂ 3	10	40	47
♀ 5.	9	41	46
♀ 6. Days 1–6 alone, fixed; on 7th joined by ♂ 5. Fully gorged on 10–12th	13	42	48

Records relating to *R. bursa* Females 1–17 (*continued*).

	Female dropped from host on day	Female ceased laying on day	Eggs began to hatch on day
♀ 7. Days 1–5 alone, fixed; on 7–12th with a ♂	12	38	47
♀ 8. Days 1–5 alone, fixed; wandered and joined on 7th by ♂ 4 ...	12	42	47
♀ 9. Days 1–3 alone, fixed; lost 4th, found 5th with ♂ 8 and afterwards with ♂ 1, ♂ 2. ½-gorged on 10th, fully gorged on 11th	13	43	48
♀ 10. Days 1–5 alone, fixed. ½-gorged 10th, fully gorged 11th ...	13	42	48
♀ 11. Days 1–4 alone, fixed; shifted and with ♂ 4 on 5th. Fully gorged on 8th	16	43	46
♀ 12. Put on 16th, with ♂ 5 on 17th, alone 18th. ¾-gorged 23rd, fully gorged 24th	25	58	63
♀ 13. Put on 16th with a wandering ♂, on 17th alone, on 19–20th with a ♂. ¾-gorged on 23rd	25	59	63
♀ 14. Put on 16th near ♂ 7 with which she copulates 17th. ½-gorged on 20th	25	58	63
♀ 15. Put on 18th, alone 19th–22nd, found loose and wandering on 23rd when put to ♂ 8 with which she copulates at once; act lasts 10 minutes; pair stay together till she drops, the male shifting next day	29	65	68
♀ 16. Put on 18th, alone till 22nd when joined by ♂ 1; the pair stay together till she drops, four males surrounding them. ½-gorged on 23rd	29	60	66
♀ 17. Put on 18th, found alone on thigh on 24th, on 35th found wandering, on 36th put on scrotum and seen to anchor herself; on 37th there are 2 ♂♂ close to her. ¼-gorged on 24th, ¾-gorged on 39th	42	78	81

The foregoing protocols demonstrate the following regarding *R. bursa*:

Males. After a preliminary feed lasting 3–5 days on one spot, the males wander in search of anchored females. Having found a female with which to copulate, the male frequently stays with her till she drops from the host and remains a day or so longer on the spot where the pair were attached. On the other hand the male may stay but a short time with a female, and seek a number of females in succession until he finds one with which to copulate. A number of males may congregate and anchor about a single female. The male may copulate with several females, a quiet feeding period of one or more days preceding copulation with a fresh female. The males wander about in search of females when no females are present upon the host, anchoring themselves in many different places for one or more days at a time. Males were observed to wander thus, in the absence of females, for a period of 86 days.

Females. All of the females were fertilized and yielded a numerous offspring. The females settle down to feed at once when placed on the host. They are sought by the males on the 4th–10th day, at times after 24 hours. A female may copulate with one or more males.

SUMMARY.

Amblyomma hebraeum males anchor immediately when placed in a hungry state upon the host. The females will not do so as a rule in the absence of previously anchored males. Usually the males do not move or scarcely move when once anchored on the host, they may continue to remain attached to the host for months after the females have dropped off gorged. The males, after having fed for a few days, show signs of sexual excitement in that they erect their bodies away from the host and extend their legs, whereby, without releasing their mouthparts from the host's skin, they seize and hold any females that chance their way. The males become excited when the skin of the host in their vicinity is handled, no females having been near them for months. To copulate, the males must necessarily release their mouthparts, and this may at times lead to their shifting their position. They may occasionally shift to a fresh anchorage in company with their females, or they may shift a few mm. when apparently alone. A male may copulate with several females. The coloration of the male changes after prolonged sojourn upon the host (77–141 days).

After feeding for 2–8 days or more, the females wander and are grasped by anchored males so that the ticks' ventral surfaces are apposed, and in this position the female proceeds to feed with her mouthparts puncturing the skin of the host in close proximity to those of the male. Copulation takes place in due course, the male temporarily removing his mouthparts from the host for the purpose. A female may seek two males in succession but usually one male appears to suffice. Females feed very slowly in the absence of males, they gorge rapidly when fertilized, and, when fully gorged, usually abandon the host without delay. Depending upon their having access to males and access to a more or less adequate food supply from the host, the females remain upon the host for 4–25 days before dropping off in a gorged condition.

Hyalomma aegyptium males anchor immediately when placed upon the host. In the absence of females they remain fixed or change their position but slightly at long intervals of time. When hungry males and females are placed together upon the host, they proceed to suck blood at once, and, after a preliminary feed lasting five or more days, the males wander in search of females. A male may copulate with several females. Females placed in close proximity to males cause these to become excited (as in *A. hebraeum*). The females as a rule do not change their anchorage upon the host from start to finish, being sought by the males. The latter stay upon the host indefinitely (122 or more days) after the gorged and fertilized females have dropped off.

Rhipicephalus bursa males and females, when hungry, proceed to feed at once when placed together upon the host. After remaining fixed for 3–5 days, the males seek anchored females. The males may seek a number of females in succession, usually feeding for some days prior to seeking a fresh female.

Males continue to wander from anchorage to anchorage in the absence of females, they may thus wander about for 86 days or longer after the females have abandoned the host. A male may copulate with several females.

The behaviour of the sexes differs therefore in the three foregoing species. In *A. hebraeum* the females seek the males, in *H. aegyptium* and *R. bursa* the males seek the females. In all three species the males remain upon the host indefinitely after the females have dropped off. In *R. bursa* the males continue to wander about from anchorage to anchorage long after the females have left, whilst in *A. hebraeum* and *H. aegyptium* the males stop their wandering entirely or shift but slightly at longer intervals of time.

The predominance of male ticks of any species upon a host under natural conditions is accounted for by their staying on and accumulating upon the host whilst successive lots of females drop off. As an example I may mention that I have seen camels in Biskra on which only males of *H. aegyptium* could be found; these males must have been a very long time upon the camels because their scutums were polished and scratched, the rugose surface so characteristic of the young male tick having been worn away.

Copulation in all three species was observed on several occasions upon the host, the process lasted 10 minutes or longer and was similar to that described by me for *Ornithodorus* and *Ixodes*.

Since the liability to injury increases with the degree of engorgement of the female tick it is a great safeguard to her that she attains her full state of engorgement rapidly at the end of her feeding period and that she drops from the host promptly.

ON TWO NEW SPECIES OF THE CESTODE GENUS *OOCHORISTICA* FROM LIZARDS.

By H. A. BAYLIS, M.A.

(With Plate XXI.)

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The cestodes of lizards have received little recent attention from systematic zoologists. Those inhabiting snakes are much better known than they were a few years ago, thanks to the researches of La Rue (1914) and of Rudin (1917). The cestodes of snakes almost all belong to the family Ichthyotaeniidae (genera *Crepidobothrium*, *Ophiotaenia*, *Acanthotaenia*). Among the lizards also, several species of *Acanthotaenia* occur in the Monitors (*Varanus*), and one is recorded in *Lialis*, one of the Pygopodidae. The Monitors are also the hosts of a remarkable genus of quite a different type—*Duthiersia*—our knowledge of which has recently been brought up to date by Beddard (1917), and of another genus—*Pancerina*—of an equally distinct type.

Among the more typical families of lizards, however, so far as we know at present, no representatives of these genera occur. On the other hand, a type represented by the genus *Oochoristica* Lühe (1898), is here prevalent. This is a genus which (as at present defined) occurs also in certain Marsupials and Edentates. It is placed near to the above-mentioned genus *Pancerina* in Ransom's (1909) scheme of classification of the Taenioid Cestodes, and is probably closely related to it, although *Pancerina* has a double set of reproductive organs in each segment, whereas in *Oochoristica* there is only a single set.

The Lacertidae and related families of lizards seem, therefore, as regards their cestode fauna, to link up on the one hand with the Varanidae, and on the other hand with the Mammalia. One species of *Oochoristica*, it should be mentioned, has also been described from a snake (*O. rostellata* Zschokke (1905), from *Zamenis*).

The species of *Oochoristica* described from lizards up to the present are not numerous, and most of the descriptions existing are far from complete. Even the type-species—*O. tuberculata* (Rud.), from *Lacerta ocellata*—has only been briefly characterised by Lühe (1898). An opportunity having presented itself, therefore, of studying two species from lizards, I have thought it desirable to describe them in some detail, especially as the genus requires better definition, and this will not be possible until more species have been fully

described. While the forms from mammals have received more attention, much confusion exists as to the limits of the genus, and it is by the study of the reptilian forms that clearer light seems most likely to be shed upon the question, since the type-species is a reptilian and not a mammalian parasite.

OOCHORISTICA ZONURI, sp. n.

Host: *Zonurus tropidosternum*. Portuguese East Africa.

External features.

This is a rather large, stout worm, measuring, in a somewhat contracted condition, up to 102 mm. in length. The maximum width is about 3 mm. The strobila is irregularly contracted, and the cuticle much wrinkled, forming deep folds between the segments. The outline of the latter is irregular in consequence, as is indicated in Pl. XXI, fig. 2. The hinder borders of the segments, as seems to be characteristic of the genus, do not overlap the succeeding segments, the division between the segments being marked externally only by a fold in the cuticle.

The scolex (Pl. XXI, fig. 1) measures 0·9 mm. across, and is not clearly marked off from the strobila. There is no trace of a rostellum. The large suckers are oval in shape, their longest diameter being antero-posterior. The outside measurements of the suckers are 0·5 mm. × 0·35 mm. The aperture of each sucker is a longitudinal slit.

The neck widens out to 1·5 mm. close behind the scolex. Owing to its contracted and wrinkled condition it is difficult to make out where segmentation begins. The segments are for the most part much broader than long; their length increases, however, relatively to their width, on passing backwards, and the gravid segments near the posterior end are nearly square. The genital pores are irregularly alternating, and situated well towards the front of the segment.

Internal structure of the Strobila.

In a transverse section (Pl. XXI, fig. 3) the medullary parenchyme is seen to occupy a little more than one-third of the whole dorso-ventral diameter, *i.e.*, the cortical parenchyme, subcuticular layer and cuticle are together thinner than the medulla. The cuticle is thick, and consists of two layers (Pl. XXI, fig. 5, C_1, C_2). The subcuticular layer contains many curious flask-shaped cells suggesting mucus-cells (Pl. XXI, fig. 5, *G.*). The inner ends of these often project beyond the other cells of the subcuticular layer into the cortical parenchyme. The parenchyme, both of cortex and medulla, is loose and contains very few nuclei.

Musculature. The longitudinal muscles consist of a single row of about 40 bundles dorsally, and 40 ventrally (Pl. XXI, fig. 3, *L.*). Each bundle contains about 15 to 20 fibres of various thicknesses. Immediately underlying the longitudinal muscles are a few fine transverse fibres (Pl. XXI, fig. 3, *Tr.*)

marking the junction of the cortical and medullary parenchyme. Numerous very fine dorso-ventral fibres run across both cortex and medulla.

Excretory system. Dorsal and ventral longitudinal vessels are present, both pursuing a very irregular and sinuous course. Both pairs of vessels are situated at some distance from the lateral borders of the segment (Pl. XXI, fig. 3, *D.* and *V.*). As seen in transverse sections, the dorsal vessel on either side is not vertically above the ventral vessel, but usually displaced a little outwardly. Narrow transverse vessels connect the ventral longitudinal pair at the back of each segment. These transverse vessels usually form a kind of "delta" at their ends, and open by several mouths into the longitudinal canal, exactly as has been described for *O. rostellata* by Zschokke (1905). They also, as in that species, often send out small side-channels along their course, forming an incipient network confined to the interproglottidal region.

Genital organs. Although rudiments of genital organs, or at least of their ducts, appear very far forward, mature segments begin to appear very late—fully 200 segments from the anterior end. There are only about eight segments with fully-developed organs before the appearance of the uterus. The latter rapidly obscures the other organs, and these very soon begin to degenerate.

In a mature segment (Pl. XXI, fig. 2) the ovary (*Ov.*) is the most conspicuous organ. It is a roughly triangular mass of lobes, not distinctly divided into two lateral portions, as is sometimes the case in this genus. Its longest diameter is from 0·4 to 0·5 mm. It lies entirely on the pore side of the middle line of the segment. The yolk-gland (Pl. XXI, figs. 2 and 3, *Vit.*) is irregular in shape, and a little smaller than the ovary. It lies obliquely behind the latter, the middle line of the segment just passing through it near its aporal end, so that the greater part of the organ is on the pore side. A small shell-gland (Pl. XXI, figs. 2 and 3, *S.*) is situated between the ovary and yolk-gland. A coiled oviduct (Pl. XXI, fig. 3, *Od.*) connects the female glands and the uterus. The latter will be described below.

The testes (Pl. XXI, figs. 2 and 3, *T.*) number from 60 to 70, and occupy the greater part of the middle field of the segment behind and at the sides of the female glands. A few on the aporal side even extend so far forward as to lie in front of the ovary. The layer of testes is only one deep, as may be seen in transverse sections (Pl. XXI, fig. 3, *T.*). The testes are mostly oval in outline, their longest diameter varying from 0·075 mm. to 0·1 mm. Their long axis most frequently lies in a direction transverse to the length of the worm.

The male and female ducts open at the base of a shallow muscular genital cloaca (Pl. XXI, fig. 2, *Cl.*). The cirrus-sac (Pl. XXI, figs. 2 and 3, *C.S.*) measures 0·25 mm. in length, and in thickness 0·2 mm. Its wall is very muscular, especially towards the outer end. The vas deferens (Pl. XXI, fig. 2, *V.D.*) is much coiled, especially about the middle of its course. The vagina (Pl. XXI, figs. 2 and 3, *Vag.*) opens into the genital cloaca behind the cirrus-sac, in the same horizontal plane. It is a very narrow tube, running almost straight towards the ovary. It does not, as in some related species, widen out at any

part of its course to form a receptaculum seminis. Both vagina and vas deferens pass between the dorsal and ventral excretory vessels and dorsal to the lateral nerve.

Remarks on the Uterus and the appearances observed in Gravid Segments.

Beddard (1914 and 1916) has remarked upon the history of the uterus and the embedding of ova in the parenchyme in certain species of *Oochoristica*, and has suggested that the study of these points may prove to be of value in deciding the difficult question of the relationships of this genus and *Linstowia*. I have paid some attention to the phenomena in question in the present species, and propose to give a brief account of the facts as far as I have been able to follow them.

The uterus (Pl. XXI, fig. 3, *Ut.*) is at first an irregularly branching thin-walled sac lying on the ventral side of the segment, near the ventral limit of the medullary parenchyme. It is flattened dorso-ventrally so that for the most part it is not capable of holding more than two layers of eggs. At first the eggs *in utero* are similar in appearance to those still in the ovary, except that they are invested by a thin membrane. Segmentation, however, very soon begins, and proceeds rapidly in the uterus. The uterine wall is very delicate, consisting of a single layer of flattened cells, indicated by scattered nuclei. The uterus sends out finger-like diverticula, containing ova, laterally as far as the ventral excretory vessels, but not beyond them. It extends nearly as far as the transverse vessels at the back of the segment, but does not reach in a forward direction as far as the most anterior testes.

The uterus only persists in this condition through a very limited number of segments—I am unable to state exactly how many. The next stage is one in which the ova previously contained in the uterus are seen to be scattered singly throughout the parenchyme. Each is now contained in a space lined by a layer of flattened cells, like those seen in the wall of the uterus. The spaces, in fact, may probably be regarded as nipped-off portions of the uterine cavity.

Some of the ova (which by now contain well-advanced embryos) now penetrate laterally beyond the excretory vessels: they also penetrate dorsally, and many may be seen lying between the testes. They do not, in this species, appear to go beyond the limits of the medulla. (In *O. marmosae* Beddard, they extend into the cortex—see Beddard, 1914.) Up to this stage, the embryo, within its parenchyme-space, is surrounded only by the thin membrane which was already present in the uterus.

Finally, in the last few segments, the testes and most of the other organs disappear, and the ova lie in a kind of honeycomb-like structure into which the medullary parenchyme has been transformed, and which may perhaps be compared (with reservations, however) with the "paruterine organ" met with in certain genera. The spaces in which the ova lie in the parenchyme appear

to have been enlarged at the expense of the parenchyme itself, which has shrunk, at the same time becoming denser, to form the walls of the honeycomb "cells." The walls of these cavities still show a few nuclei, but their cellular nature is not at all obvious. The ova now contain a definite six-hooked embryo, which is surrounded by three membranes: (1) its original membrane; (2) a rather thick brownish shell, secreted (by the embryo?) since its embedding in the parenchyme; (3) an outermost membrane, usually much crumpled in the sections, and staining deeply with haematoxylin. This seems to be derived from the wall of the parenchyme-space, to which it is sometimes still adherent. This account of the egg-membranes agrees completely with that given by Zschokke (1905) in the case of his *O. rostellata*, but, curiously enough, not so well with Beddard's (1914) description of *O. marmosae*. In the latter case only two membranes were found, apparently corresponding to the first and last of the three mentioned in the present form. In *Linstowia ameivae*, on the other hand (described in the same paper), Beddard found all three membranes.

Abnormal Segment.

A case of abnormal reduplication of the genital organs in a single segment was observed in this species. The segment (Pl. XXI, fig. 4), which is that immediately preceding the three shown in Pl. XXI, fig. 2, contains two sets of female glands, two genital pores, one on either side of the segment, two vasa deferentia and two vaginae. This condition is probably brought about by the fusion, or incomplete separation, of two consecutive segments, as is indicated by the positions of the two sets of female glands; these are so placed that the organs on the left are somewhat in front of those on the right, and seem to belong to what would have been the anterior of the two segments. This explanation is borne out by the number and arrangement of the testes. These show a more or less clear division into two sets corresponding to the two segments. There are too many testes for one segment, but not quite the full complement for two. (82 were counted, of which about 60 seem to belong to the posterior segment, and the remainder to the anterior.) A line drawn across the segment in the direction of the dotted line in the figure would probably coincide very nearly with the missing division.

OOCHORISTICA AGAMÆ, sp. n.

Host: *Agama* sp. Africa.

Oochoristica truncata (Krabbe, 1879) from *Agama sanguinolenta*, has recently been re-described in detail by Rudin (1916). This author has fully substantiated Zschokke's (1905) view (as to which there could not be much question) that Krabbe's "*Taenia*" *truncata* was an *Oochoristica*. It may also be considered fairly certain that Rudin's species is identical with Krabbe's, since in both cases the host was specifically the same. Hitherto *O. truncata* was the only species of the genus recorded from *Agama*. My material, however,

differs to such an extent from Rudin's description that it evidently represents a distinct, though closely allied, species.

The following account is based to a certain extent on two sets of specimens. The first is from *Agama* sp. from Portuguese East Africa. The preservation of these examples is unfortunately somewhat imperfect, and, probably in consequence of this, they have been a good deal stretched and distorted. This would account for certain apparent differences from the other and better-preserved specimens, which will be mentioned below. They are also hopelessly tangled together, so that it is almost impossible to obtain complete specimens.

The second set was found among the collections in the British Museum, bearing the label "*Agama* 428. 10. 4. 92." There is unfortunately no further definite information as to the source of these specimens, but it is believed that they formed part of a collection from Africa. There can be no doubt that both sets belong to the same species; the following description, however, except where otherwise stated, is taken from individuals of the second set, the preservation of which is sufficiently good for detailed study by means of sections.

External features.

The longest specimen measures 80 mm. in length. The maximum width is about 1·5 mm. The cuticle shows the same tendency to form wrinkles and irregularities as was observed in *O. zonuri*, and there is the same absence of the overlapping hinder borders of the segments. The scolex measures 0·45–0·65 mm. across, and has no rostellum. The suckers are circular in outline, and measure 0·175 mm. in outside diameter. There is a short unsegmented neck, but, as in *O. zonuri*, it is difficult to see exactly where segmentation begins. The anterior segments, as far back as the earliest in which signs of the uterus appear, are considerably broader than long. When the uterus reaches its full development, they become squarish, and from this point backwards they gradually elongate, the posterior segments becoming from two to three times as long as broad. The genital pores alternate irregularly, and are situated a little in front of the middle of the lateral margin of the segment.

Internal structure of the Strobila.

In transverse sections the medulla occupies about one-third of the total dorso-ventral diameter. The cuticle, subcuticular layer and parenchyme present the same characters as have been described in the case of *O. zonuri*.

Musculature. The longitudinal muscles are very slightly developed. There is an inner layer of from 25 to 30 small bundles both dorsally and ventrally, each bundle consisting of about 6 to 8 fibres. At about the middle of the thickness of the cortex there is a separate outer layer of still smaller bundles, with at most three or four fibres in each, and sometimes the bundle is represented merely by a single fibre. The same transverse and dorso-ventral fibres are present as in the former species.

Excretory system. Of the two pairs of longitudinal vessels, the dorsal pair are very narrow, but thick-walled. They are usually situated vertically above the ventral vessels, but may be a little to either side of them. The ventral vessels are very wide. These, instead of being merely connected by a branching transverse vessel at each interproglottidal division, as in *O. zonuri*, give off numerous small lateral branches, which ramify about and anastomose here and there, forming a complete network extending throughout the medullary parenchyme.

Genital organs. Rudiments of the genital ducts are visible in almost the earliest distinguishable segments. Mature segments appear at about the 35th. The ovary (Pl. XXI, fig. 6, *Ov.*) is situated almost in the centre of the segment. It consists of two large lateral portions connected by a narrower bridge, and the whole, when fully developed, measures from 0·23 to 0·25 mm. across at the widest part. Behind it is the yolk-gland (Pl. XXI, fig. 6, *Vit.*), forming with the two lateral portions of the ovary, as Lühe (1898) remarks to be characteristic of the genus, very much the shape of a trefoil-leaf. Between the ovary and yolk-gland, on the dorsal side, is the shell-gland (Pl. XXI, fig. 6, *S.*).

The testes (Pl. XXI, fig. 6, *T.*) are from 39 to 46 in number. In the best-preserved material (Pl. XXI, fig. 6) they are arranged almost in a straight series of three to four rows across the back of the segment. They extend forward a little further at the sides than in the middle of the series, but not as far forward as the yolk-gland. In the other material (Pl. XXI, fig. 7), where the segments have been much stretched in a longitudinal direction, they surround the yolk-gland in a horse-shoe pattern. This difference is probably sufficiently accounted for by the different states of contraction. The two figures referred to are drawn to the same scale, and the apparent difference in the size of the testes is due to one of the segments not being at quite such an advanced stage as the other.

The genital ducts pass between the dorsal and ventral excretory vessels and dorsally to the lateral nerve. They open at the base of a large muscular genital cloaca (Pl. XXI, fig. 6, *Cl.*), 0·15 mm. long. The cloaca has a narrow distal portion and a large proximal cavity, into which the fleshy cirrus protrudes from the cirrus-sac. The walls of the cloaca send out many radiating muscle-fibres to the subcuticular layer. The cirrus-sac (Pl. XXI, fig. 6, *C.S.*) is of an elongate pear-shape. It measures about 0·15 mm. in length and 0·08 mm. in width at the widest part, which is nearest to the cloaca. The vas deferens (Pl. XXI, fig. 6, *V.D.*) is much coiled for the distal portion of its course. The vagina (Pl. XXI, fig. 6, *Vag.*) enters the genital cloaca behind and somewhat ventrally to the cirrus-sac. It forms a spindle-shaped swelling in its course before reaching the ovary, then becoming narrow again. Between the two lateral portions of the ovary it forms a coil functioning as a receptaculum seminis.

The uterus begins to appear at about the seventh mature segment. Its

earliest rudiment is a flattened sac with thin cellular walls, lying just ventrally to and in front of the ovary. It rapidly sends out egg-containing processes, at first in front and at the sides of the ovary, and eventually all over the segment, as far as the limits of the medulla. This stage is reached within about six segments, and the ova then become scattered throughout the parenchyme. The history of the uterus and egg-cavities, in fact, appears to be almost precisely as in the species already described, the chief difference being the more forward position occupied by the uterus. The ova go through the same stages in the formation of their envelopes, and have a precisely similar appearance. When fully developed, the outer membrane measures about 60 μ in diameter, and the onchosphere itself 37 μ.

It may be useful now to give a simple key for the separation of the three forms from lizards to which special attention has been given in this paper. They may be simply distinguished as follows:

A. Maximum width of strobila over 2 mm.
Testes more than 60 in number ... ... *O. zonuri.*

B. Maximum width of strobila less than 2 mm.
Testes less than 60 in number

B 1. Width of scolex less than 0·4 mm.
Transverse excretory vessels simple ... ... *O. truncata.*

B 2. Width of scolex more than 0·4 mm
Transverse excretory vessels form an elaborate network *O. agamae.*

OOCHORISTICA and LINSTOWIA.

As Beddard (1914 and 1916) has pointed out, there seems to be very little ground for the separation of these two genera, and certainly no justification for placing them in separate families. In endeavouring to find some difference of generic value, this author says (1914): "One structural feature occurs to me as being of possible use in better defining the two genera.... But it is so little known that it cannot be used for the present and may after all turn out to be worthless. This concerns the imbedding of the ova in the parenchyma after the disappearance of the uterus." He then goes on to explain that the kind of difference meant is that shown by the two forms that he has just been describing—*Linstowia ameivae* and *Oochoristica marmosae.*

The points of difference mentioned by Beddard, as regards the uterus and egg-capsules, may be briefly summarised as follows (supplemented in one particular from Beddard's observations (1913) on another species of *Oochoristica* from the *Tamandua* Anteater).

Oochoristica (*marmosae*).	*Linstowia* (*ameivae*).
Uterus at first a well-marked posterior transverse tube, with lateral diverticula.	Uterine cavities from the first less strongly marked off, and do not form a coherent group.
These have well-marked walls, though no special lining.	Walls of cavities not definite.

Oochoristica (*marmosae*).	*Linstowia* (*ameivae*).
Ova from the first confined to the uterine cavities.	From the first some of the ova are found in the parenchyme *between* the uterine cavities.
Uterus persists through a good many segments.	Uterine cavities exist for a much shorter period. "The uterus seems to be degenerating...as compared with that of *O. marmosae*."
Oochoristica sp. from *Tamandua*.	
Egg-containing spaces in parenchyme have a definite cellular wall. (Figured by Beddard, 1913, p. 875, text-fig. 149.)	Egg-containing spaces have no definite cellular wall at any stage.

These characters, it must be admitted, are by no means definite—indeed, Dr Beddard evidently puts them forward chiefly as affording a possible means of separating off the South American forms parasitic in mammals from other species of the two genera. As he states, "it is... next to impossible to separate the genera if we accept the present distribution of species among them."

As regards the characters afforded by the uterus and the egg-capsules, the two species here described do not seem to afford much help in defining the limits of the genus. On the whole, they agree better with the account of *O. marmosae* than with that of *L. ameivae*, but there are certain points in which they diverge from it. Thus there is a definite, though very thin, cellular lining to the walls both of the uterus and of the parenchyme-spaces; yet the latter are not thick-walled embryo-sacs such as Beddard has described and figured for the species from *Tamandua*, which is ascribed to *Oochoristica*. Again, the arrangement of the egg-membranes, as already noted, is like that of *Linstowia ameivae* and of *Oochoristica rostellata* Zschokke, and unlike that of *O. marmosae*.

Other characters such as the relative thicknesses of the cortical and medullary parenchyme, and whether the testes do or do not extend across the whole of the dorsal side of the segment from back to front, are, as Beddard concludes, probably of little value in distinguishing between the genera. There are, however, two points mentioned in Ransom's (1909) diagnoses, which might on further investigation prove to be important. These concern the arrangement of the genital pores, and the course taken by the genital canals. The former are said to be irregularly alternating in *Oochoristica*, and regularly so in *Linstowia*. The vas deferens and vagina, in *Linstowia*, are said to pass ventrally to both pairs of excretory vessels and to the longitudinal nerves, while in most of the species[1] ascribed to *Oochoristica* in which the point has been studied (though this is not mentioned by Ransom), they follow the more usual course between the dorsal and ventral vessels and dorsal to the nerves. This at least is the case in *O. rostellata*, *O. truncata*, *O. zonuri*, *O. agamae* and Beddard's species from *Tamandua*[2].

If a distinction is to be made at all, it seems not unlikely that the name

[1] In certain forms from Marsupials and Edentates the genital ducts are said to pass *dorsally* to the excretory vessels.

[2] Beddard (1914) does not mention this point in the case of *Linstowia ameivae* and *Oochoristica marmosae*.

Oochoristica will have to be reserved for the forms from reptiles (including, probably, *Linstowia ameivae*), and perhaps certain of those from mammals, such as the *Tamandua*-species; while the rest of the mammalian forms will be assigned to *Linstowia*. In any case, it seems clear that all these forms ought to be included in the same subfamily, instead of, as at present, in separate families. Without attempting to go into the question fully at present, it may be said that on a general view of their characters both genera seem to belong rather to the Dilepinidae than to the Anoplocephalidae, among which one of them (*Linstowia*) is at present placed.

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EXPLANATION OF PLATE XXI.

Fig. 1. *Oochoristica zonuri*. The scolex, much magnified.

Fig. 2. *O. zonuri*. Three consecutive mature segments (from a whole preparation). *Cl.*, genital cloaca; *C.S.*, cirrus-sac; *Ov.*, ovary; *S.*, shell-gland; *T.*, testes; *Vag.*, vagina; *V.D.*, vas deferens; *Vit.*, yolk-gland.

Fig. 3. *O. zonuri*. Transverse section through a mature segment in which the development of the uterus has begun. *C.S.*, cirrus-sac; *D.*, dorsal excretory vessel; *L.*, longitudinal muscles; *N.*, longitudinal nerves; *Od.*, oviduct; *Ov.*, ovary; *S.*, shell-gland; *T.*, testes; *Tr.*, transverse muscle-fibres; *Ut.*, uterus; *V.*, ventral excretory vessels; *Vag.*, vagina; *Vit.*, yolk-gland.

Fig. 4. *O. zonuri*. Abnormal mature segment, containing two sets of reproductive organs. (From a whole preparation.)

Fig. 5. *O. zonuri*. Portion of a transverse section through the cuticle and subcuticular layer, very highly magnified. C_1, C_2, outer and inner layers of the cuticle; *C.M.*, circular muscle-fibres; *G.*, glandular cells; *L.M.*, longitudinal muscle-fibres; *P.*, cortical parenchyme.

Fig. 6. *Oochoristica agamae*. Mature segment (from a whole preparation). *Cl.*, genital cloaca; *C.S.*, cirrus sac; *Ov.*, ovary; *S.*, shell-gland; *T.*, testes; *Vag.*, vagina; *V.D.*, vas deferens; *Vit.*, yolk-gland.

Fig. 7. *O. agamae*. Mature segment (from a whole preparation), showing the alteration in the apparent relations of the genital organs due to stretching of the tissues in imperfectly preserved material.

TSETSE FLIES AND TRYPANOSOMIASIS.

SOME QUESTIONS SUGGESTED BY THE LATER HISTORY OF THE SLEEPING SICKNESS EPIDEMIC IN UGANDA PROTECTORATE.

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PART I.

I. HISTORICAL.

The actual commencement of the great wave of human trypanosomiasis, which claimed so many thousands of lives along the shores of Lake Victoria, is difficult to determine. The attention of Europeans was first attracted to the disease early in 1901, when eight cases of sleeping sickness were admitted to Mengo hospital by the Drs Cook, who had been established in Uganda some five years, to whom the clinical picture was quite new. Enquiry among the chiefs of Buganda revealed the fact that sleeping sickness was known to the natives as *mongota*, and was more prevalent in the eastern portion of the Pro-

tectorate than in Buganda itself. A large number of deaths had already occurred in Busoga Province and in Buvuma Island.

The existence of this name, *mongǫta*, in the Luganda language is of itself strong evidence that an identical or similar disease existed previous to the recognition of sleeping sickness in 1901. There is no evidence that the word was coined to fit a previously unknown complaint. It is possible, however, that several more or less obscure diseases may have been confused in the general application of the name.

From a general biological point of view it seems probable that some form of human trypanosomiasis had existed in the Victoria Nyanza fly zone previous to the epidemic. So far as is known, in no other part of Africa is fly and man in such intimate contact as in this region. The disease is endemic in the Gambia, in the Congo, in Nigeria and along the shores of Lake Tanganyika, in fact in all places where *Glossina palpalis* occurs in any degree of contact with human beings.

Enquiries instituted in connection with the early days of the Uganda epidemic elicited the fact that the disease occurred within the Protectorate in various *palpalis* areas, along the Nile, around lakes Edward and George, and in the 'Mpologoma region. It was supposed to have spread to these localities from the great lake, or, in the case of the Nile area, from the Congo. There is however at any rate a possibility that the disease in these districts had existed for years and was only recognised in consequence of the careful search which resulted from the epidemic.

On this explanation, also, regarding man merely as a mammal susceptible to trypanosomes, we should expect to find a certain degree of tolerance in the natives of such a thickly infested fly area as the northern shores and islands of Lake Victoria.

The sudden increase in the number of cases of *mongota*, in some of which somnolence was perhaps not a marked feature, the terrible mortality and consequent disorganisation of food supplies were all unprecedented. Such a combination of circumstances was indeed "unknown to the natives," although typical sleeping sickness cases might be recognised as *mongota*.

To return to the Uganda epidemic, however, it is known that from 1898 to 1900 there was a great deal of distress in Busoga and on Buvuma Island coincident with drought and failure of crops, and attended by a considerable mortality. Before July, 1901, there was no medical officer in Busoga, and very little was known of the dense and lawless populations of this Saza and the neighbouring Buvuma Islands. It may well be that cause and effect were confused in assigning this mortality to the famine which, in reality, both masked and accentuated the effects of the disease.

II. THE ASSUMPTIONS ON WHICH SIR H. HESKETH BELL BASED HIS SUPPRESSIVE MEASURES.

In November, 1906, as a result of the investigations which were carried out by the various Commissions appointed for the purpose, H.M. Commissioner and Acting Governor Sir H. Hesketh Bell put forward a scheme for dealing with the disease.

He assumed that, unless something drastic was done to check the spread of the epidemic, the whole population of the fly area would die of sleeping sickness. He based his measures mainly upon the following assumptions:

(1) "That there are no authenticated instances of the transmission of the disease from sick persons to healthy, in districts where the tsetse fly is not found" (1).

(2) "That the presence of even a single diseased person in a locality infested by tsetse flies may entail the infection of the whole community" (1).

(3) That "the disease, so far, appears to be incurable" (1).

(4) That "the tsetse fly was the indispensable link in the chain of infection, and that only by the elimination of that link could the spread of the disease be checked" (2).

(5) That an enormous percentage of the population of the fly zone was already infected with the disease and that on certain islands the entire population had disappeared (3).

(6) That "the decrease in the number of deaths in the kingdom of Buganda since 1903 is not believed to have been due to any diminution in the virulence of the disease, but simply to the reduction of possible victims in the infected areas" (4).

The order of arrangement of the above six assumptions has no reference to Sir H. Hesketh Bell's reports, nor to order of precedence.

He aimed at extermination of the disease as the extermination of the fly appeared to be unobtainable. His measures entailed the removal inland of the whole surviving populations of a two mile zone of the mainland shore line and of the islands, away from all possible contact with the fly. At the same time those actually suffering from the disease were to be segregated in various camps throughout Buganda and Busoga, also outside the fly zone.

The segregation of the sick was commenced in December, 1906 (5). By the end of 1907 the mainland population had been removed inland, and, from the German border on the west to the Ripon Falls on the east, the coastal zone to a depth of two miles had been cleared of inhabitants.

During 1908 similar measures were completed in Busoga and in 1909 the islanders were removed from Buvuma and the Sesse group. It was hoped that after the disappearance of the disease, which was expected to follow these measures, the surviving populations would be able to return to their old homes.

These measures were enforced only within the limits of Uganda Protectorate. Different policies prevailed in the neighbouring fly areas of German East Africa and British East Africa. The Germans combined deforestation measures with a limited depopulation scheme applied to certain particularly "dangerous" localities. In British East Africa the natives were left in contact with the fly, an attempt to encourage voluntary segregation and isolation from the fly proving abortive.

III. OUTCOME OF THE MEASURES.

As a result of these measures the most sanguine hopes were realised as regards the stamping out of the disease in the fly zone of Uganda Protectorate.

In British East Africa, along the shores of the Kavirondo Gulf, the epidemic apparently worked itself out after causing a very heavy mortality. The disease in this area now appears to be endemic and the population is reported to be again increasing.

As regards German East Africa the authorities there described the measures pursued as "completely successful," yet they admit that isolated cases of fresh infection occurred from time to time.

IV. EXAMINATION OF THE AVAILABLE STATISTICS BEARING ON THE EPIDEMIC.

The figures quoted here are derived from official returns from the P.M.O.'s office and the Secretariat at Entebbe.

In endeavouring to arrive at a true conception of the percentage of deaths to the total population exposed to the fly, data from the islands afford much more definite and reliable information than do figures from the mainland. Except on the big island of Buvuma, nowhere on the islands could the natives get more than 2½ miles from the shore, and there was constant canoe traffic between the various islands and with the mainland, to say nothing of wholesale fishing.

On the mainland, however, a large proportion of the population lived well outside the fly zone. Some might never see a tsetse fly and others only very occasionally be exposed to fly bite.

The total number of deaths returned as by sleeping sickness in the kingdom or province of Buganda, including the Sesse and Buvuma Islands, from 1900 to the end of August, 1915, is as follows:

1900	8,430	1908	1,783
1901	10,384	1909	925
1902	24,035	1910	547
1903	12,891	1911	253
1904	11,251	1912	82
1905	8,003	1913	57
1906	5,304	1914	24
1907	3,407	1915	2[1]

[1] Since 1915 the deaths by sleeping sickness in Buganda Kingdom or Province have been very few—exact returns are not available at time of writing.

The returns from 1900 to 1903 are doubtfully exact. The figure for 1902 is probably too high. The deaths during 1903 have been recorded as 30,441, but an error was found in the compilation of the original returns. After 1903 the returns are more reliable. It is probable, however, that the maximum number of deaths occurred in 1902, as indicated by the table, and thereafter declined.

In 1906 it was not believed that this decline was due to any diminution in the virulence of the disease but "simply to the reduction of possible victims in the affected areas." It was also believed that all the inhabitants of the Sesse and Buvuma Islands were not only "possible victims," but that they were nearly all (90 per cent. or over) actually infected in 1906–1907. Until 1909, when the islands were depopulated, and the survivors removed to the mainland, the number of inhabitants was not known, nor was any exact count kept of the number of Buvuma islanders removed during that year. The number of Sesse islanders removed was exactly recorded as 11,776 and this gave, for the first time, a secure basis for estimating the number of deaths per thousand for the years immediately preceding and succeeding. The population of the Buvuma Islands was estimated to be "barely 14,000" in 1906, and the number of islanders removed in 1909 was estimated by the officer in charge of the operations to have been 11,000. The number removed has also been stated to be between 5000 and 6000, but we cannot find any basis for this estimate, and regard the larger figure as probably more nearly correct. It is thus possible to secure some idea of the death-rate per thousand among the Sesse and Buvuma islanders, both before and subsequent to their removal, as shown by the following table.

Table, showing deaths returned as by sleeping sickness among the Sesse and Buvuma islanders, with estimated number of islanders and deaths per thousand.

	Buvuma Islanders			Sesse Islanders		
Year	Deaths by sleeping sickness	Estimated number of islanders	Indicated number of deaths per thousand	Deaths by sleeping sickness	Estimated number of islanders	Indicated number of deaths per thousand
1900	5,137	56,322	91	789	23,166	39
1901	6,874	51,185	134	1,048	22,377	47
1902	19,049	44,311	428	1,950	21,329	91
1903	5,174	25,262	205	2,549	19,379	132
1904	3,503	20,088	175	2,238	16,830	133
1905	2,585	16,585	155	918	14,596	63
1906	1,001	14,000	71	718	13,578	52
1907	1,314	12,981	99	678	12,960	52
1908	667	11,667	55	506	12,282	41
1909	258	11,000	23	436	11,776	37
1910	93	—	8	188	—	16
1911	67	—	6	84	—	7
1912	25	—	2	11	—	1
1913	15	—	1	8	—	1
1914	6	—	1	7	—	1

Despite numerous chances for error it is plain from the above table that following the climax of the epidemic there was a great reduction in the number of deaths per thousand of "possible victims" prior to 1909 when the survivors were removed from contact with tsetse. A decline is indicated by each year's death returns except for the year 1907, when an increase is recorded among the Buvuma islanders and no decrease indicated among the Basesse. This is explained by the fact that the mainland shore was depopulated during this year, and that the natives possessing canoes and dependent on fishing moved (with their sick) to the islands, instead of moving inland, away from the lake shore. This caused a sharp increase in the number of deaths recorded from the islands, which is complemented by a corresponding decrease in the number of deaths recorded from the mainland. If allowance were made for this, it would indicate an even greater decline in deaths per thousand among the "possible victims" than indicated by the table, the errors in which are mostly on the conservative side.

The steady decline in the virulence of the epidemic as indicated by the declining number of deaths in Buganda Province was only in part due to reduction in number of "possible victims"; for all the islanders were regarded as in this category and the number of deaths per thousand among them was declining only a degree less rapidly than the total number of deaths. If this had been as evident prior to 1909 as it subsequently became, it is doubtful if such drastic measures would have been adopted for "preventing spread" of infection.

There is no doubt that there prevailed in the minds of those engaged in investigating the epidemic, between 1902 and 1906, an impression that a relatively enormous percentage of the population of the fly zone was already infected, and therefore doomed.

Thus Gray, speaking of the Buvuma in a report on the work done at the sleeping sickness camps up to the end of November, 1907, states "I am inclined to a belief that, if a systematic examination was made of the inhabitants of these islands, the percentage of infected persons would be found to be 95 per cent. if not more (6). Of the Basesse, Koch in 1906 expressed the opinion that nine-tenths of the natives who were living in the archipelago seemed to be already infected and that, failing the discovery of a therapeutic cure, all would die" (7).

When the question of segregation camps was first considered, Koch was of the opinion that nine camps would not be sufficient to accommodate all the sick. Events proved that four were amply sufficient.

These impressions were undoubtedly based on the presumption, proved correct in many instances, that all cases of trypanosome fever developed into sleeping sickness. This assumption was strongly sustained by report and by the belief that the disease was literally exterminative locally, as on some of the Sesse and Buvuma Islands, leaving no survivors. It is a point of great importance, however, that no large number of individual cases was detected

and kept under observation, and apart from the reported extermination of local populations, there is no evidence that all cases developed into sleeping sickness, or proved eventually fatal.

V. THE JUSTIFICATION FOR THE PREVENTIVE MEASURES.

Sir H. Hesketh Bell declared in recommending the suppressive policy that "only the seriousness of the situation could have warranted such drastic measures" (8). It is indeed true that only a most serious situation could have justified measures which involved the complete expatriation of whole tribes of natives; the wholesale destruction of property—huts, plantations, canoes, fishing gear, etc., and even of live stock; and the, temporary at least, destruction of all economic values throughout a territory which for natural wealth might be compared to the Protectorate of Zanzibar, and which had been originally as populous as the Gambia.

Nevertheless these measures were entirely justifiable on the assumption that a close parallel existed between human and bovine trypanosomiasis, between "sleeping sickness" of man and "fly sickness" of cattle as transmitted (in Uganda) by *Glossina palpalis* and *Glossina morsitans* respectively. This assumption received additional support from the discovery that the trypanosome responsible for the human disease was, also, like that causing cattle disease, a parasite of fly and game in uninhabited country. It was common knowledge that in order to control bovine trypanosomiasis it was necessary completely to sever all contact between fly and cattle. Nothing could have been more natural than to assume that similarly drastic measures were necessary to check the spread of the human disease.

VI. EARLY CRITICISMS OF THE MEASURES.

It was predicted in certain quarters that it would prove impracticable completely to sever all contact between fly and population; that fly could not be completely exterminated from localities, such as the lake ports, where it was inexpedient to remove the population; and that natives could not be altogether prevented from trespassing on depopulated territory. Therefore, it was predicted that the disease could not be extirpated, but would persist endemically, ready to spread as soon as reoccupation of fly infested territory was attempted. This forecast was made before it was known that the parasite could persist in fly and game.

This criticism of the measures proposed, it will be noted, is based on the same premises as the argument used in support of them, and assumes, in effect if not in direct reference, the existence of an exact parallel between human and bovine trypanosomiasis.

The criticism is of particular interest in view of the outcome of the measures. It was in fact proved to be impracticable completely to exterminate fly from populated districts or completely to prevent trespassing and poaching in the depopulated zone; but despite the fact that measurably broad contact between

population and fly continued, sleeping sickness has been practically, if not completely, wiped out from those parts of Uganda adjoining Victoria Nyanza.

Thus both the exponents and the critics were in part justified by the outcome, and in part confused by it, for both had based their arguments on the belief that complete severance of contact was necessary in the case of human, as in that of bovine trypanosomiasis, and this is proved to be unnecessary.

VII. COMPARISON BETWEEN BOVINE AND HUMAN TRYPANOSOMIASIS IN UGANDA.

The following comparison may now be drawn between bovine trypanosomiasis as transmitted by *G. morsitans*, and human trypanosomiasis, as transmitted by *G. palpalis* in Uganda.

(*a*) Points of similarity disclosed by technical research:

Both diseases are caused by trypanosomes which are parasitic on game and tsetse flies. In both cases the parasite undergoes an "endogenous" reproductive cycle in the vertebrate host and an "exogenous" reproductive cycle in the insect. In both cases the parasite is transmitted by the insect in the act of feeding.

(*b*) Points of dissimilarity disclosed by the outcome of the measures for the suppression of sleeping sickness:

Cattle cannot be herded in territory infested to a measurable degree by straggling flies of *G. morsitans* without grave danger of infection and death, but densely gathered populations have existed for years (as at the lake ports) in territory infested by *G. palpalis* to an easily measurable degree, and no cases of sleeping sickness are known to have resulted. Cattle cannot wander or stray for even an hour or two into territory thickly infested by *G. morsitans* without grave danger, but many poachers and trespassers wander and stray into territory densely infested with *G. palpalis* and no cases of sleeping sickness are known with certainty to have resulted.

If a herd of cattle is driven into or through a region infested by *G. morsitans*, some animals are almost sure to become infected and die, even though exposure to fly lasts for no more than an hour or two; but large parties of natives have been sent on expeditions into territory infested by *G. palpalis*, and have resided there continuously for many months, and it is not certain that any cases of sleeping sickness have resulted.

It is plain from this comparison that the parallel between "fly sickness" of cattle and "sleeping sickness" of man is by no means so exact as would naturally be expected, in view of the points of similarity disclosed by the technical research in the laboratory. In consequence it does not appear necessary, for practical purposes, to resort to such extreme measures for the control of the human disease as are necessarily used for controlling the cattle disease.

PART II.

VIII. THE TSETSE FLY AS A TRANSMITTER OF HUMAN TRYPANOSOMES.

There are two ways in which a human trypanosome may be transmitted to a man by fly:

(1) By the direct method.
(2) By cyclical transmission.

(1) *Direct or "mechanical" transmission* of *T. gambiense* by *G. palpalis* has been proved to occur. It is known, both from field observation and laboratory experiment, that an interruption before it has finished its feed makes *G. palpalis* doubly eager to resume and complete its meal. In the case of man there is, so far as is known, no other biting fly whose mouthparts are adapted to the transmission of trypanosomes which can compare with the *Glossinae* as a disseminator of the disease by the direct method.

Conditions ideal for direct transmission of trypanosomes existed in the closely packed canoes of Victoria Nyanza.

(2) *Cyclical transmission.* Here the trypanosome undergoes a cycle of development in the fly. During the earlier stages of this cycle the insect is incapable of conveying the parasite to susceptible hosts upon which it feeds. A condition is finally produced when the parasite is established in the salivary glands of the fly which is henceforward infective, as far as known, until its death.

There is a large amount of evidence to show that in only a small percentage of *Glossina palpalis* is the trypanosome capable of undergoing cyclical development. The highest percentage of positive flies that we have obtained in any laboratory feeding experiment was 20·6 (9). Miss Robertson (10) gives 3·4 as the average percentage of positive flies given with the Uganda strains of what is generally presumed to be *T. gambiense* in laboratory bred flies. Frequency of the infecting feedings appears to make no difference in the resulting percentage of positive flies. In the above percentage calculations any fly showing multiplication of trypanosomes in its gut is classed as positive. A large proportion of these, however, died before the invasion of the salivary glands with infecting forms had occurred.

In the course of the investigations of the Commissions of the Royal Society a large number of experiments have been carried out to determine the percentage of wild flies carrying the polymorphic trypanosome, which appears from laboratory evidence identical with the organism which caused the epidemic. Experiments conducted with wild flies caught near Entebbe in 1903, where the natives were considered to be infected with trypanosomes in the proportion of 1 in every 3 or 4, revealed a percentage of 0·3 positive flies; 0·1 per cent. of positive flies resulted from experiments performed in May, 1911, with wild flies from Damba Island, in the Sesse group.

IX. COMPARISON BETWEEN *G. PALPALIS* AND *G. MORSITANS* AS VECTORS OF MAMMALIAN TRYPANOSOMES.

Glossina palpalis feeds freely on reptiles. It shows distinct preference for certain reptiles (crocodiles and *Varanus*) over many mammals, and notably for reptiles over man. Reptiles do not, as far as we know, harbour in nature the species of trypanosomes pathogenic to mammals. *G. morsitans*, on the other hand, feeds most freely on game animals and is not known to attack reptiles nor freely to attack birds. It follows that, of a given number of flies of each species, a larger proportion of *morsitans* than of *palpalis* is likely to ingest mammalian trypanosomes.

There is a considerable amount of evidence to show that, after ingestion by the fly, mammalian trypanosomes are more likely to complete their cyclical development and render the insect permanently infective if the fly continues to feed on mammalian, and particularly a ruminant, than if it feeds on reptile blood. It is to this extent more likely that mammalian trypanosomes will complete cyclical development in *G. morsitans* than in *G. palpalis*. Although *G. palpalis* shows a distinct preference for other hosts over man, *G. morsitans* appears to be as freely attached to cattle as to its most favoured hosts among the game animals. There is a proportionately greater likelihood that infective *morsitans* will attack oxen than that infective *palpalis* will attack man.

Briefly, a smaller proportion of flies is likely to ingest mammalian trypanosomes, and of the flies ingesting them a smaller proportion is likely to become infective in the case of *G. palpalis* than of *G. morsitans*. Also, of the flies which do become infected, a smaller proportion is likely to transmit infection in the case of *G. palpalis* than of *G. morsitans*—to man and the domestic ruminants respectively.

But despite the small proportion of infected *G. palpalis*, and despite the relative immunity of man to attacks by fly, there are yet enough flies infective and enough men attacked to make it almost incredible that some men are not attacked by infective flies each year. It seems certain that some natives have been attacked each year and that cases of trypanosomiasis have resulted without being detected, or else that the parasite is much less virulent to man in its present condition than it is believed to have been when sleeping sickness was epidemic.

It is also difficult to believe that many cases of sleeping sickness could have developed without detection, but this does not apply to trypanosome fever which might very easily escape notice if it failed to develop into sleeping sickness.

It is, therefore, a plausible hypothesis that, in its present state, the trypanosome (as a parasite of fly and game) is less virulent to man than formerly; and that, as transmitted to man by fly deriving it from game, it either fails to infect or causes only a mild and chronic form of disease.

X. THE PART PLAYED BY EACH OF THE ABOVE TWO METHODS OF TRANSMISSION IN THE PERPETUATION OF TRYPANOSOME STRAINS.

The trypanosomes on entering the gut of a fly suited to their cyclical development multiply enormously by division. This process is continued for at least 17 days and finally the forms infective to a new host are found in the salivary glands of the fly. The gulf separating these salivary gland forms from the original infecting trypanosomes is, biologically speaking, enormous. It is reasonable to suppose that none but specific and deep-rooted characters could survive such a drastic ordeal. The question of the transmission of acquired characters through the insect intermediary has not yet been properly worked out for the haematozoa. Gonder's experiments with *T. lewisi* are, however, most instructive in this connection (11). He found that a strain of *lewisi* whose resistance to arsenic had survived 20 passages, lost this property when transmitted cyclically by lice. The same strain when transmitted by the lice from rat to rat by the direct method retained its arsenic resistance.

Laboratory strains of trypanosomes are almost invariably kept up by various methods of subinoculation, which may be said to correspond nearly to direct transmission by the insect intermediary. Many of these laboratory strains acquire in the course of time atypical characters. In the case of Yorke and Blacklock's *T. vivax* strain, the organism eventually acquired the power of survival in rabbits, which animals were wholly resistant to the earlier passages (12).

Instances of increase in virulence of laboratory trypanosomes are not uncommon; this is notably the case with certain *gambiense* and *brucei* strains. We know, however, of no evidence to show that these characters, acquired in the course of prolonged direct transmission, can persist when exposed to the searching processes involved in cyclical development in the insect host.

There is no apparent reason why such specially virulent strains should not be developed in nature whenever mechanical transmission is sufficiently free. It may be that an example of this is afforded by the direct transmission of cattle disease, such as that caused by *T. pecorum*, by insects incapable of cyclical transmission of the trypanosome but which, none the less, cause outbreaks away from tsetse fly.

The conditions necessary for direct transmission are primarily the presence of large biting flies (small biting flies such as mosquitoes, *Simulium*, etc., are not suspected to transmit trypanosomes in this manner), and, incidentally, in view of the difficulty of transmission, the presence of many large biting flies and of many potential hosts of the parasite in close juxtaposition.

These conditions are met with when an infected ox is admitted to a herd grazing in a densely fly infested pasture, and it is only under such conditions, so far as we are aware, that epidemics of fly sickness occur. They would also be met in the case of game animals, such as buffalo, which run in herds, and which are subject to attack by large biting flies of "common" species.

Under such conditions we have every reason to expect that strains of trypanosomes may sometimes develop in nature through repeated "mechanical" transmission, comparable in their animal reactions to strains developed in laboratories.

In this case we have something more than mere possibility or plausibility to go upon—it is a definite probability that search will reveal the existence of such strains in nature. Moreover the development of such a strain might well be signalled by some "outbreak" or "epidemic" of trypanosomiasis in a vertebrate host ordinarily resistant to the normal strain of the parasite, such, for example, as the epidemics of virulent human trypanosomiasis which swept the Nile basin. Here would be a distinctly plausible explanation for various circumstances—for the recovery of the infected islanders—for the curiously prompt and complete disappearance of the virulent type of the disease—for the sustained virulence of the virulent type, and absence of evidence suggesting any gradual change in it—for absence of any irrefutable evidence that the virulent type can be transmitted from game or domestic animals to man—for the almost complete absence, in fact, of any positive evidence that a "cyclically" infected fly ever transmits true "sleeping sickness" to man.

We must recognise the probability that strains of fly-borne trypanosomes of acknowledged virulence may sometimes be developed naturally, and cannot disregard the possibility that such a strain actually developed to cause the great epidemic of sleeping sickness. It is curious, if not significant, that we can find no evidence in negation of what at first appeared a highly improbable hypothesis.

The crew of a native canoe illustrates well the importance of direct transmission in the Uganda epidemic. In these canoes any number from two to twenty and more natives might work for hours in close juxtaposition.

When a canoe is pushed off from a fly infested shore (and the canoe landings on Victoria Nyanza were notoriously densely infested), or if it passes close in to such a shore, a small—and sometimes a large—swarm of flies will come off and follow it to open water. The flies will not come off to a passing canoe more than one hundred yards or so from shore, neither will they freely leave a canoe that they have followed to a greater distance from shore, but will accompany it for hours. Under these conditions more may feed on the crew than if the same crew remained on the beach, and it is the commonest sight under these conditions to see one paddler after another dislodge a biting fly, which, in the course of a few minutes, may have bitten several men.

Conditions for "mechanical transmission" are absolutely ideal—as favourable in proportion to the number of flies involved as could be reproduced in the laboratory. It is proved by laboratory experiments that this species of fly can transmit this species of trypanosome with a certain facility under such conditions; and it is not only possible or plausible, but virtually certain that mechanical transmission in canoes must have occurred with frequency and regularity during the early stages of the epidemic.

The riparian populations of Uganda possessed many hundreds, probably several thousand, canoes, which were in constant use for fishing and commerce. They also fished, in parties, from fly infested shore; gathered in numbers for repairing canoes, fishing gear, etc., under similar conditions; and finally there were market places where islanders met mainlanders for exchange of produce, at points on the shore that were well known to be densely and dangerously infested by fly.

PART III.

XI. CONCLUSIONS TO BE REACHED REGARDING THE TRYPANOSOMES PRESENT IN MAN AT THE TIME OF THE EPIDEMIC FROM A CONSIDERATION OF THE MORTALITY STATISTICS.

It has been shown that the death rate among the surviving island populations, after their removal in 1909 up to the outbreak of war, was only from 4 to 6 per cent. of the total number removed. What then are the logical conclusions to be derived from this statement?

They are either that the assumption that 90 per cent. of the population were already infected is wrong or that all those infected did not die.

We have no grounds for discrediting the estimated proportion of infected persons and must accept, provisionally at least, the statement of officials who were in a position to know the facts. Therefore we must conclude, provisionally, that very many infected persons recovered.

This conclusion is difficult to reconcile with the statement and common belief that on some islands the epidemic reached an exterminative culmination and left no survivors, or so few as to seem a negligible quantity. On some islands, we are informed, there was approximately or actually 100 per cent. of infections, and that all persons, old and young, developed sleeping sickness and died(13); whereas on other islands, after the climax of the epidemic had passed, there were 90 to 95 per cent. of infections but more than 80 per cent. of recoveries.

As before we must, provisionally at least, accept the statements and common belief of officials who were in a position to know the facts, and this leaves no alternative to the conclusion that the trypanosome was subject to great variation in its pathogenicity toward man.

This conclusion must now be reconciled with the statement and common belief of persons in a position to know, that the disease showed no signs of diminished virulence in individual cases(14). Reconciliation is only possible on the assumption that sleeping sickness showed no signs of diminution in virulence, but that the number of cases of trypanosome fever which failed to develop into sleeping sickness was very much greater on some islands, toward the close of the epidemic, than on other islands or perhaps generally, during the earlier stages of the epidemic.

This provisional conclusion agrees well with the common belief held in 1906–1907 that trypanosome fever always developed into sleeping sickness. Possibly it may have done so in a much greater proportion of cases in the earlier stages of the epidemic than in the later years.

It also adds plausibility to the hypothesis that, at present, the trypanosome persisting in fly and game is less virulent toward man than that responsible for the decimating epidemic of sleeping sickness: in short, that we have to deal with two types of human trypanosomiasis, one chronic and the other invariably fatal, caused respectively by two different strains of the parasite. The fatal strain naturally burnt itself out. The other, causing a generally mild, though possibly sometimes fatal, disease, is relatively widespread and persistent.

XII. GENERAL CONCLUSIONS.

In the preparation of a paper of this character we have had three main objects in view:

(1) To call attention to the fact that the bio-economic problem created by the tidal wave of sleeping sickness that swept the region of the Upper Nile in general and the shore of Victoria Nyanza especially, is not solved, but that it has merely passed from the stage which called for measures designed to prevent further destruction of life and values into a new stage calling for the substitution of reconstructive for preventive measures. The "main and most important feature" of the measures adopted in Uganda in 1907 was to remove all natives from contact with the fly in order to prevent further spread of the disease and further destruction. The main and most important feature of the reconstruction measures must be to replace the populations and recover economic values, but at the same time to preclude absolutely the possibility of another devastating pestilence. This effort toward reconstruction is in every respect as important and necessary as the effort to prevent further destruction.

(2) To call attention to the main question raised by the outcome of the preventive measures, with a view to determining future policy. Are we justified in accepting the most obvious interpretation and proceeding to reconstructive effort on the assumption that an epidemic of sleeping sickness is impossible unless there is sufficiently broad contact between fly and population to render possible the development of a virulent, "mechanical transmission," strain. Or must we take also into account the possibility that the pathogenicity of the trypanosome may be subject, *per se*, to variations, irrespective of the method by which it is transmitted? On this latter explanation the disappearance of acute trypanosomiasis in Uganda is not altogether due to the preventive measures, but also in greater or less degree to diminution in pathogenicity of the parasite and that the trypanosome is liable to resume a virulent state, even in Uganda Protectorate, under existing conditions.

(3) To present the results of self-questioning along these lines, which has resulted in the formation of a working hypothesis supported by considerable

negative, but relatively little positive evidence, and which for the present is chiefly valuable as it suggests the need for further specific enquiry.

Pending the results of such enquiry this hypothesis affords the best answer we can give to what we regard as the main question. It recognises the possibility that *T. gambiense* may vary greatly in pathogenicity to man: it takes into account the manner in which peculiarly virulent strains of normally less virulent species of insect-borne trypanosomes are developed: it recognises also the real probability that such strains may develop in nature as well as in the laboratory: it recognises a clear possibility that a peculiarly virulent strain of *T. gambiense* may have been developed in this manner; and, finally, if it could be proved well founded, it would indicate that very broad contact between fly and population is a prime essential to the occurrence of sleeping sickness in the form of a widespread epidemic.

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ON THE LIFE-HISTORY AND LARVAL ANATOMY OF *MELINDA COGNATA* MEIGEN (DIPTERA CALLIPHORINAE) PARASITIC IN THE SNAIL *HELICELLA* (*HELIOMANES*) *VIRGATA* DA COSTA, WITH AN ACCOUNT OF THE OTHER DIPTERA LIVING UPON MOLLUSCS[1].

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(With Plates XXII—XXV and 6 text-figures.)

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[1] Published with the aid of a grant from the Government Grant Committee, Royal Society.

INTRODUCTION.

THIS paper consists of two parts: (I) a complete account of the life-history and a description of early stages of *Melinda cognata* Meigen which I found here in Cambridge living as parasites on a common snail, *Helicella virgata* da Costa, and (II) a review of all observations made hitherto on the life-history of different flies feeding upon living or dead molluscs.

Acknowledgments: I am much indebted to Mr C. J. Wainwright for the identification of my specimens of *Melinda cognata* Meig. and those of sarcophagids. I owe also to him, and to Dr J. Villeneuve, valuable information concerning different species of *Onesia* flies. I am grateful to Dr Th. Becker for the identification of some of my specimens of Phorids and the description of a new species of *Phora*. The identification of different snails I owe to the kindness of Mr H. H. Brindley. Finally I have to acknowledge the very friendly assistance rendered by Mr F. Balfour-Browne in revising my manuscript for the press.

I. SYSTEMATIC POSITION OF THE GENUS *MELINDA* ROB.-DESV. AND ITS RELATION TO THE GENUS *ONESIA* ROB.-DESV.

Before we begin the study of the life-cycle of *Melinda cognata* Meig. it is important to deal with the systematic position of this fly.

The genus *Melinda* was founded by Robineau-Desvoidy in 1830 for a few species of flies which he placed near the genus *Calliphora* in his group of Diptera ovipara. Later on, Schiner (1862) and almost all other entomologists placed the genus *Melinda* as a synonym of the genus *Onesia* which was also created by Robineau-Desvoidy. In 1901, Hendel came back to the old idea of Robineau-Desvoidy in separating from *Onesia* a few species under the generic name of *Melinda*, but most entomologists although agreeing that *Onesia* contained two groups of species, those of the *cognata* type and those of the *sepulchralis* type, nevertheless continued to place all these species in one genus.

As we shall see presently, the separation of the genus *Melinda* from *Onesia* is sustained not only by differential characters of the adult flies but also by a comparative study of their life-history and larval morphology.

As on the other hand, these two genera were confused, the different characters of the species of one genus were often wrongly used in making generalisations regarding species belonging to the other genus.

Therefore, to avoid confusion, we should examine separately and in chronological order all we know of the life-history of species belonging to the genera *Onesia* and *Melinda*.

(*a*) Onesia Rob.-Desv. (1830). Characters of the genus and life-history.

Characters of the Imago. Plump greenish flies; feathering of arista short and confined to basal portion, much as in Sarcophaga; cheeks wide; alulae covered with dark hairs as in Calliphora; male genitalia large and prominent; two post-sutural intraalar bristles; three strong sternopleural bristles; claws and pulvilli of male elongated.

Life-history.

Geoffrois and Robineau-Desvoidy (1830) were the first to find that these Diptera are viviparous. For *O. sepulchralis* this was also stated by Schiner (1862, p. 576). The latter adds that *Onesia* larvae live upon animal substances, but his statement is merely based on analogy and not upon actual observation.

During my research on *Pollenia rudis* F. (1915 *a*, pp. 91–105) the larvae of which live as parasites in the earthworm, I often noticed that the worms *Allolobophora foetida* Eisen., *caliginosa* Sav. and *chlorotica* Sav. contained in their vesicula seminalis a few first stage Dipterous larvae other than those of *Pollenia*. These larvae were always dead and surrounded by phagocytes. Being at first unable to identify them, I called them by a letter *A*. Subsequently, I found that the worms which usually contained these larvae (*A*) showed also third stage larvae occupying in the host the same position as those of *Pollenia rudis*.

But, unfortunately, when these larvae left the earthworms they were infested and killed by a fungus thus making it impossible for me to identify them. I called these third stage larvae by the letter *B* supposing them to belong to the same fly as larvae *A*.

Finally, on dissecting some *Onesia* females from the Cambridge Entomological collection, I found that the flies contained in their uterus nearly 250 well-formed larvae which proved to be identical with larvae *A*, thus showing that the first stage larvae of *Onesia* penetrate into the vesicula seminalis of different species of common earthworms.

As to their ultimate development, all I can say at present is that if the third stage larvae *B* belong to the same species of fly as larvae *A*, the life-history of *Onesia* should be similar to that of *P. rudis*, *i.e.* from the vesicula seminalis of the earthworm, the first stage *Onesia* larva migrates to the host's prostomium, this is perforated by the insect's posterior end so that its spiracles communicate with the air. In this position the larva passes through two moults or three stages, destroying the earthworm more or less completely.

This is all that we know at present of the life-history of the genus *Onesia*.

(*b*) MELINDA ROB.-DESV. (1830). CHARACTERS OF THE GENUS AND PREVIOUS KNOWLEDGE OF LIFE-HISTORY.

Characters of the genus (Pl. XXII). Flat, blue coloured flies. Feathering of antennae as in Calliphora. Alulae free from hairs; male genitalia small, withdrawn almost from sight; three post-sutural intraalar and two strong sternopleural bristles; claws and pulvilli in male not elongated; cheeks narrower than in *Onesia*.

Life-history.

According to Robineau-Desvoidy these flies are oviparous. This statement is solely based upon the observation that the abdomen in the female does not contain larvae as does that of *Onesia*.

In 1909, Pavay-Vajna stated that the larvae of *M. cognata* Meig. cause subcutaneous myiasis in the young of the White Wagtail (*Motacilla alba*). From his note, to which I referred in detail in an earlier paper (1915 *a*, pp. 95–96), I will only restate the following:

The observations of Pavay-Vajna were made in Hungary (Olahlapad, Komitat Alsó-Fehér) where he found a nest of *M. alba* containing four young birds upon which were pitted wounds. In one of these wounds was a Dipterous larva which soon pupated; the imago emerging 13 days later was identified by Kertesch as *Onesia cognata* Meig. All the young birds died within one to four days after this observation.

In 1917, Father Schmitz, in the course of his research upon *Drilus flavescens*, frequently noticed the appearance of adult flies of *Melinda cognata* Meig. in the breeding vessels containing livingsnails (*Hygromyia hispida* L., *Patula rotundata* Müller, *Hyalinia cellaria* and others) collected as food for the larvae of the beetle. On May 28th he collected, near Maastricht, a dozen living snails, and, on June 4th, one of these (*Patula rotundata*) died, and from it there emerged a larva which duly pupated. From this pupa on June 25th–26th emerged an imago, which was identified by Dr Villeneuve as *Melinda cognata* Meig.

According to Schmitz, the observation of Pavay-Vajna is based upon an error in the identification of the Insect. This opinion is also expressed in the letters which I have received from Drs Villeneuve and Bequaert. As the identification of Pavay-Vajna's specimen was made by Dr Kertesch, I would hesitate before doubting its correctness, but regarding Schmitz's observation we may consider the occurrence of *M. cognata* on *Motacilla alba* as merely accidental.

II. LIFE-HISTORY OF *MELINDA COGNATA* MEIGEN[1] PARASITIC IN *HELICELLA* (*HELIOMANES*) *VIRGATA* DA COSTA.

Last year I found in and around Cambridge the larvae of *M. cognata* living in a small snail, *H. virgata*. I was able to determine the relation between the parasite and the host, to follow the complete life-cycle of the fly, and to study the anatomy of its larva.

(*a*) The host.

Helicella (*Heliomanes*) *virgata* da Costa is a small snail varying greatly in size, shape and colour. It is very common in England, Wales and Ireland, and it occurs in France, Corsica, etc. It is gregarious and often appears in thousands covering the pastures and the hedges. In this connection the following statement of E. Steep (1901) is of interest.

> The Banded Snail is widely distributed in England, Ireland, and Wales, but in Scotland appears to be found only in Ayrshire. It is most abundant along the south coast, especially in Cornwall, on Dartmoor, and along the South Downs. To get an accurate idea of its profusion in these parts it is advisable to walk out on the pastures after heavy summer rain; then one can excuse the local idea that these snails come not from among the herbage but from the heavens, as though they were hailstones. Fences, gates, stones, thistles, and grass stems are so thickly coated with them that one marvels how it is possible for them to find cover or food at other times. These molluscs have long been regarded as the source of the flavour peculiar to the Down mutton, but I think it is usually considered that they are eaten inadvertently by the sheep in cropping the short grass. I am assured by intelligent Cornish farmers, however, that this is not so: when sheep are turned out to feed on the cliff-pastures they make by preference for those parts near the edge where the "*sheepsnails*" (*H. virgata* and *H. acuta*) are most plentiful, and they thrive exceedingly upon them. They do not appear to hibernate. Full-grown specimens measure a little more than half an inch across.

According to Macquin-Tandon (1855) *H. virgata* lays in autumn 30–60 eggs from which the young hatch in 15–20 days. They become adult in the middle of the second year.

The specimens used for this study were collected in or near Cambridge in the following places: hedgerows in Grange Road, Barton Road, Grantchester Road, along the footpath from Grantchester to Barton, Madingley Road and

[1] As previously mentioned, the flies of *Melinda* which I bred from snails were identified by Mr C. J. Wainwright to be the common species *M. cognata* Meig. Since, on the other hand, the type of *M. cognata* Meig. has not been recently examined, Mr Wainwright thinks it is important to specify that this common British species is what Kramer and Villeneuve regard as *cognata* and which Strobl and Schiner called *gentilis* Rob.-Desv., but that it is not the species which the latter describe as *cognata*.

M. cognata of Schiner and Strobl corresponds to *gentilis* Rob.-Desv. as described by Verrall (*Ent. Monthly Magaz.* 1912, p. 192). Until Meigen's type is examined, to place the identity of my specimens beyond doubt, Mr Wainwright advises me to call them *M. cognata* (Meigen?) Kramer =*gentilis* Schiner and Strobl).

along the Hills Road near the "Gogs[1]." In all these places, and especially along the footpath mentioned above, a great number of the snails contained *Melinda* larvae. It is interesting to note that in all these places, and especially along the Grantchester Road, this snail was found in the company of *Helicella itala*, *H. cantiana*, *Hygromyia rufiescens*, *Helix nemoralis* and *H. hortensis* but in no case were any of these species parasitised by the fly. Further, a white non-banded variety of *H. virgata* found in abundance along the iron fence between the Caius ground and Church Rate Walk, seemed to have escaped the attack of the fly, as I collected several hundreds of specimens on different days and never found *Melinda* larvae. On the other hand I found the larvae in the same variety of snails collected in other places.

(*b*) MELINDA COGNATA MEIG. AND ITS LIFE-CYCLE.

As previously mentioned, Robineau-Desvoidy placed this fly (*M. cognata*) among the oviparous Diptera. Most probably he relied upon the fact that dissection of the female never revealed the existence of larvae as one would expect to find in a viviparous insect. But the real proof of oviparity or viviparity is to see the eggs or larvae at the time they are laid. I have often found the eggs of *Melinda* in ones or twos or very rarely threes in the mantle cavity of *H. virgata* near the Bojanus organ or kidney of the host (*ov.* Pl. XXIII, fig. 3). They were usually in different stages of development, one being newly laid while the other contained a well-developed embryo, or there might be an egg and one or two larvae showing that all the eggs had not been laid at the same time. Unfortunately I was never able to observe the actual deposition of an egg, but I imagine that the fly oviposits near the pneumostome, or directly in the mantle cavity, as the pneumostome is often widely open especially when the snail is in motion, but even in the snail contracted within its shell it opens and closes rhythmically. It is probable that the most favourable time for infection is during the copulation of the snails, when the latter are incapable of rapid contraction, but infection certainly takes place at other times also, as I have found *Melinda* larvae in immature snails.

From the egg there emerges a small larva which by means of its strongly chitinised mouth-parts bores its way into the kidney of the host where it lies with its posterior end protruding into the mantle cavity or pulmonary cavity of the snail (*L.* Pl. XXIII, fig. 3). This position is obviously connected with the fact that the larva is metapneustic and requires to keep its only pair of spiracles exposed to the air.

During this stage the larva feeds upon the fluid of the kidney and destroys the renal epithelium the cells of which contain crystals of ammonium urate. Thus the alimentary canal of the parasite becomes filled with these crystals.

So far, the snail shows no signs of distress, one cannot distinguish a healthy snail from an infected one without removing it from its shell. If this is done,

[1] I have to express here my best thanks to Capt. J. Munro for kind help in collecting the snails.

however, one can see through the transparent tissues the flattened or folded empty egg-shell lying in the posterior end of the mantle cavity, and, in the posterior end of the kidney can be seen the moving mouth-parts of the larva, these appearing as a small black spot. The rest of the larva is difficult to see but sometimes its posterior end is visible when it projects from the kidney into the mantle cavity (*L.* Pl. XXIII, fig. 3). Within the kidney, the larva passes through its first moult, the excuvia, including the mouth-parts of the first stage, remaining by its side.

During the *second stage* it grows rapidly, enlarges the kidney and lies in the mantle cavity with its ventral side toward the shell of the snail. It thus assumes a curved position, its ventral side being convex and following the curve of the shell, but the spiracles always remain in communication with the air, being directed towards the pneumostome of the mantle cavity (*L.* Pl. XXIII, fig. 1). The snail may still retain its activity and may be seen moving about slowly, but more frequently it fixes itself to a plant and lies retracted in its shell.

The larva now moults a second time and passes to its third and final stage. It becomes very active and voracious, entirely destroys the kidney, attacks the liver, and its effect upon the host becomes very distinct. The snail no longer moves about but is always retracted within its shell which is sometimes fixed upon a plant but more frequently lies loose upon the ground.

The larva grows rapidly and soon occupies the whole length of the mantle cavity whilst it projects its posterior end through the pneumostome into the external air (*L.* Pl. XXIII, fig. 6).

In the meanwhile the walls of the mantle cavity have become shrunken and have presumably ceased to function, although the snail is not yet dead as is shown by small contractions of the foot and of the region surrounding the pneumostome.

All the organs of the host are attacked in turn. The liver, which is very fragile, is destroyed, the alimentary canal is perforated, and the snail ultimately dies before the larva is full grown.

One knows with what rapidity a snail decomposes after death. Within two days of its ceasing to show any movements the animal is transformed into a strongly smelling decomposed liquid mass forming the final meal of the parasite which thus ends by being saprophagous.

As previously mentioned, while feeding upon the living snail, the larva lies with its ventral side towards the shell and assumes a curve by which that side is convex, and it is interesting to note that this curve is retained even when the larva is lying free in the putrefying remains of the host.

As the food supply is exhausted, the larva works its way into the upper whorl of the shell which it completely occupies. During the whole of the saprophagous period, the posterior spiracles of the larva remain in communication with the external air.

If one of the shells containing the larva in this stage is broken, and its contents emptied into a dish with some water, a transparent tube, many times

the length of the larva, will be found coiled around it and attached by one end to its anus. This tube, which is the peritrophic membrane, is fairly resistant and keeps the excrement separated from the putrefying snail which is the food of the larva.

The larva, when full grown, leaves the shell, penetrates into the earth, and by the next day it becomes a pupa from which about 14 days later the adult emerges.

I endeavoured to find out the duration of each stage of the larval life but did not succeed because it was impossible to discover by any external signs whether or not the snail was parasitised. Had I found the Church Rate Walk snails at a sufficiently early date I would have dissected out the eggs and different larval stages from parasitised snails and inserted these in the unparasitised ones; but, by the time I discovered this apparently immune colony, the parasite was too far advanced in its development. I can only say that the development from egg to pupa is completed in about 15 days so that the whole life-cycle occupies about a month. I found the parasitised snails during June to September, but, as in June the snails contained some advanced larvae, it is probable that the life-cycle begins in May. The rapidity of the larval development indicates that *Melinda* probably passes through three generations in the year. The species hibernates in the pupal stage since I have found pupae during the whole year.

I mentioned previously that a snail may contain two or three larvae in different stages of development but only one of these larvae succeeds in completing its life-cycle. The others are always killed; the surviving larvae biting the others and possibly sucking them by accident; the brown scar of the bite can be seen on the deflated skins of dead larvae.

The parasitised snail cannot rid itself of the parasite. I never found a *Melinda* larva mechanically expelled from the snail nor phagocytised in the host's body as was often the case with *Pollenia rudis* in the earthworm (cf. Keilin, 1915 *a*, pp. 50–57).

Attempts to obtain eggs under artificial conditions were unsuccessful. A large number of males and females of *Melinda*, bred out from the snails and enclosed in a muslin cage, were fed with sugar and honey which they readily took. At intervals I dissected females but in no case did I find the ovaries developed or spermatozoa in the spermathecae. In all the females the fat body was largely developed, and this condition persisted from August until December by which time I had exhausted my material. Pl. XXV, Fig. 16, shows the state of the internal genital organs of one of these females.

(*c*) HYMENOPTERA HYPERPARASITES OF *M. COGNATA*.

As parasites of *Melinda cognata* Meig. I can only mention two Ichneumonids, which were kindly identified by Mr Claude Morley as *Atractodes exilis* Hal. and *Exolytus petiolarius* Thomson. Very little is known of the life-history of these Hymenoptera. In Morley's book on British Ichneumonids there is

only mentioned that the author found *Atractodes exilis* in August 1901 "swarming on *Heracleum* flowers in an ordinary meadow, at Lyndhurst in the New Forest." There is no record of the habits of *Exolytus petiolarius* which are only known to visit the flowers of *Angelica sylvestris*. And, referring to the whole genus *Exolytus*, Morley writes (p. 254) that "very little is at present known of the economy of this genus, though both Brischke's record of *E. laevigatus* from Tenthredinidae and Thomson's of *E. incertus* Först. from Syrphid larvae point to its relation with the Tryphoninae." These two Ichneumonids: *A. exilis* Hal. and *E. petiolarius* Thomson were bred by me under the following conditions:

Several parasitised snails of *H. virgata* were collected bearing the third stage larvae of *M. cognata*; they were kept in the laboratory in a jar covered by muslin. The *Melinda* larvae soon pupated and from the pupae emerged several imagines of *Melinda*, two specimens of *A. exilis* Hal. and two of *E. petiolarius*.

This shows us that the Ichneumonids oviposited in *Melinda* larvae when the latter were still in the snail. The oviposition probably takes place either when the larva protrudes the posterior end of its abdomen from the pneumostome of the snail, or when it lays free in the decomposed mass of its host.

III. DESCRIPTION OF THE EARLY STAGES OF *MELINDA COGNATA* MEIG.

(*a*) The egg of the parasite, extracted from the mantle cavity of its host, is elongated, slightly curved, and 1·1 mm. long (Pl. XXIII, fig. 4 *a*), it is white, has a very fine granulated surface, the markings being in the form of elongated hexagonal cells (fig. 4 *b*).

(*b*) First stage larva.

As in almost all Cyclorhaphous Diptera, the larva passes through three stages separated by two moults. The first stage larva when full grown is about 2·6 mm. long. The fat cells being poor in reserve material, the larva is transparent and consequently its internal organisation is easily seen through the skin. The larva has a small head or pseudocephalon, three thoracic and eight abdominal segments (Text-fig. 1). The head, as is the case in all Cyclorhaphous larvae, is divided in its anterior portion by a deep median groove into two lateral lobes which bear each a rudimentary bell-shaped antenna and a slightly prominent maxillary palp, the latter composed of a number of sensory papillae.

On the ventral side of the first thoracic segment and near its anterior border are several series of black chitinous hooks with the points directed backwards. The meso- and metathoracic segments bear similar series of hooks but on these two segments they are smaller in size and fewer in number. Each of the first seven abdominal segments bears on its ventral surface two series

of similar hooks: one towards its anterior margin and with the points directed backwards, the other towards its posterior margin and with the points directed forwards. Thus each of the intersegmental grooves of the abdomen are bordered by two series of hooks with their points pointing in opposite directions (Text-fig. 2). This disposition of hooks is similar to that in the primary larva of *Pollenia rudis* (Keilin, 1915 *a*, p. 69) and in both cases it enables the larva to fix itself in the tissues of its host. On the ventral surface of the eighth or last abdominal segment is the anus which is in the form of a cleft surrounded by a perianal protuberance, while above and behind this are the only pair of functional spiracles which the larva possesses. The spiracles communicate with the lateral tracheal trunks through a "felt-chamber" which is a short tube filled with a spongy chitinous structure.

Fig. 1. First stage larva of *Melinda cognata* Meig. seen from the side.

As the anatomy of the larva does not change very much during its development, I shall describe it in connection with the third stage. I shall confine myself here to a description of the mouth-parts as these are the only structures which differ considerably in the different stages.

The *Buccopharyngeal armature* is composed of the following parts (Pl. XXIV, fig. 7):—the basal or pharyngeal sclerite (*b.scl.*), which is strongly chitinised, its posterior lateral emargination (*l.e.*) through which the dilator muscles of the pharynx are visible, being very deep and wide. Anteriorly this sclerite becomes narrow and lengthens out into a chitinous plate which lies vertically in, and protrudes from the mouth, its anterior edge being sharpened like the blade of a knife. This anterior plate forms the labrum (*Lbr.*) of the larva. Ventrad to this anterior plate is another smaller sclerite, connected with it near its base and close to this connection the single salivary duct (*s.d.*) opens into the floor of the pharynx. The sides of this ventral sclerite are strongly chitinised and its anterior portion is thickened to form the labium (*lbm.*). On either side of the mouth is a "lateral hook," a flattened chitinous structure with a strongly dentate ventral edge (*l.h.*). These lateral hooks, hinged upon the sides of the ventral sclerite, are moved by extensor and retractor muscles, the motion of the hooks being in the vertical plane of the larva, their function being to scratch or hold on to the tissues of the host while the labrum cuts its way forward.

Fig. 2. Intersegmental portion of the first stage larva of *Melinda cognata*.

In the first stage *Melinda* larva the labrum is ankylosed with the basal plate so that the whole of this structure is moved as one piece when the

labrum is being used as a cutting instrument. In *Pollenia rudis* on the other hand, the labrum is articulated with the basal plate and thus moves independently (Pl. XXIV, fig. 12).

(*c*) Second stage larva (Text-fig. 3).

The average length of the second stage larva is 7 mm. During this stage the larva is more opaque than in the first stage but its internal organs are still visible by transmitted light. The three thoracic segments, near the anterior border, show a few series of hooks with backwardly directed points, while each of the first five abdominal segments bears two series of hooks as in the previous stage. The three last segments show only the posterior series of hooks. The larva has now become amphipneustic, and the anterior prothoracic spiracles usually bear four to six short papillae (Pl. XXV, figs. 15, 17 and 25).

Fig. 3. Second stage larva of *Melinda cognata* seen from the side.

In some cases there are four or five of these papillae on the one spiracle and five or six on the other. I described a similar case in the larva of *Muscina assimilis* Fall. (1917, p. 410).

The structure of the postabdominal spiracles is the same as in almost all the Cyclorhaphous larvae (Pl. XXV, figs. 23 and 24). There are two spiracular tubercles and each possesses two oval clefts surrounded by a peritreme (*per.*) of irregular form. Near the outer border of this peritreme is a small white spot which marks the external opening of the perispiracular glands (*o.*) and this opening is surrounded by a series of chitinous hairs expanding in the form of a fan. Each spiracular tubercle, near its internal border, shows a scar (*sc.*) which represents the opening through which the tracheae of the previous larval stage were expelled.

Occasionally an abnormal spiracle is found in which one of the peritremes is double so that the tubercle has the appearance normal to the third stage larva (Pl. XXV, fig. 24, cf. also a similar abnormality in the third stage, p. 441 and Pl. XXV, fig. 21).

The *Buccopharyngeal armature* (Pl. XXIV, fig. 10) has now the appearance which is very usual in Cyclorhaphous larvae. The above mentioned figure shows clearly its structure and the relations of the different parts to one another. The basal sclerite is large and the floor of the pharynx, as in all parasitic Dipterous larvae, is without the longitudinal ridges which are so well developed in saprophagous larvae (cf. Keilin, 1915 *a*, pp. 127–142).

(*d*) Third stage larva.

The full-grown larva, when ready to pupate, is 12 mm. long and 0·6 mm. in diameter; the boundaries between the segments are not clearly marked and

the skin shows also supplementary folds which mask the real segmentation of the body (Text-fig. 4).

The chitinous hooks, which are small and transparent, vary in shape and there are all the transitions between a real hook-like process on the one hand and wide flattened scale on the other; these hooks or scales are disposed in series of sinuous rows.

The sensory organs of the skin are either in the form of small pits surrounded by chitinous rings, or in the form of hairs; the latter being in six groups, each composed of three hairs, which represent the remains of the thoracic legs, and are connected with the imaginal discs of these legs (cf. Keilin, 1915 *a*, pp. 166–173).

The larva is amphipneustic, the anterior, prothoracic spiracles are composed of five papillae (Pl. XXV, fig. 26) similar to those of the second stage. Each of the postabdominal spiracles (Pl. XXV, fig. 20) bears three oblong clefts surrounded by oval peritremes having the internal border dentate; the peritremes lie so that their axes converge towards the scar (*sc.*). The spiracular tubercle shows also four openings (*o.*) of perispiracular glands, which, as in the previous stage, are surrounded by divergent chitinous hairs. In a few cases these spiracles were abnormal, one peritreme being smaller than the other two (Pl. XXV, fig. 21). A similar abnormality was observed by Nielsen (1909, Pl. II, fig. 18 and Pl. III, fig. 49 *b*) in a third stage larva of *Ptychomyia selecta* Meig.

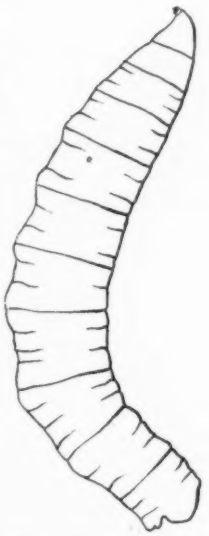

Fig. 4. Third stage larva of *Melinda cognata* seen laterally.

The *Buccopharyngeal armature* is of the same general structure as in the previous stage (Pl. XXIV, fig. 9) but it is much larger and the basal sclerite (*b.scl.*) shows, near the pharynx, a supplementary emargination, which is narrow and deep, thus marking out a small triangular plate (*t.*). The two lateral hooks (*l.h.*) are narrower and more slender than those of the second stage.

For the details of the structure of this organ I need only refer to Pl. XXIV, Fig. 9 which shows also the reduced antennae (*an.*), maxillary palpe (*m.p.*), and radiating furrows of the cheeks.

The alimentary canal (Pl. XXV, fig. 14). The pharynx (*ph.*) is followed by a short oesophagus (*oe.*), which, after passing through the nerve ring, penetrates the proventriculus (*pr.*) forming the oesophageal valve. Four short coeca (*c.*) arise from the anterior portion of the midgut, just behind the proventriculus. The midgut (*m.g.*) is very long and sinuous so that it is very difficult to trace its course. The two pairs of Malpighian tubes arise at the

junction of the mid- and hindgut. The salivary glands (*s.gl.*) are elongated, extending to nearly half of the length of the larva, their posterior ends being embedded in a patch of a fat-body.

(*e*) Puparium and pupa.

The puparium (Pl. XXIII, fig. 5) is of a brown colour, oval and with clearly marked segments. The prothoracic spiracular horns (*h.*) of the pupa emerge from the puparium through a pair of holes on its latero-dorsal side near the intersegmental space which separates the first and the second abdominal segments. These horns (Pl. XXV, fig. 19) bear a great number of small spiracular papillae and each horn communicates with a long "felt-chamber" (*f.c.*) which, near its basal portion, inside the puparium, bears an internal spiracle (*i.sp.*). This latter has the form of a bifurcated tubercle bearing papillae upon each process.

IV. THREE OTHER FLIES LIVING UPON *HELICELLA VIRGATA* DA COSTA.

(*a*) *Melinda* sp. probably *M. gentilis* (R.-D.) Verrall (1912)[1].

In the kidney of several living specimens of *Helicella virgata* there occurred a first stage larva of another Calliphorine of which unfortunately I could not obtain either the other stages or the adult. This larva occupied the same position in the host as the larva of *M. cognata* and very often the two occurred simultaneously in the same host.

The anatomical study of this larva revealed its striking resemblance to that of *M. cognata*; in fact it differs from the latter only in the form and the size of the external cuticular hooks or spines and a few details in the structure of the buccopharyngeal organs. As shown in Pl. XXIV, fig. 8, the medio-dorsal sclerite or labrum (*Lbr.*) is more prominent, pointed, and curved dorsally; the lateral hooks (*l.h.*) are larger and more strongly chitinised. It is very probable that this larva belongs to *Melinda gentilis* which is also a very common species in England. The fact that these larvae occur less commonly in *H. virgata*, and are always killed by the larvae of *M. cognata* indicates that this snail is not their usual host. As on the other hand the different species of snails which I collected with *H. virgata* did not contain this larva, it is possible that the real host of *M. gentilis* is a *Limax* or an *Arion* as the slugs were common in all the places where I collected the *H. virgata*.

(*b*) *Sarcophaga nigriventris* Meig.

Böttcher, in his paper on the genus *Sarcophaga* (1913, p. 367) quotes Villeneuve as authority for the statement that Prof. A. Giard, in September 1906, bred *S. nigriventris* from a snail, *H. cantioniformis*, collected near Wimereux in the Pas-de-Calais.

[1] *Melinda gentilis* R.-D. described by Verrall (1912) = *cognata* of Schiner and Strobl.

Another record on the habits of this very common species of Sarcophagid is contained in a short note of E. W. Bowell (1917), published in the *Proceedings of the Malacological Society of London*. The note is as follows: "Some time since I found a number of dead and moribund *H. itala* on the common by Chipstead Station in Surrey which are apparently being destroyed by some dipterous larvae. Some of the imagines were bred out, and have kindly been identified by Mr K. G. Blair of the British Museum as *Sarcophaga nigriventris* Mead. The causes of the death among the Mollusca are so little understood that this identification seems worth recording."

From several specimens of *H. virgata* killed by the larvae of *Melinda cognata* and also from dead and decomposed specimens of *Theba cantiana* I extracted the full-grown larvae of a Sarcophagid from which the adults of *S. nigriventris* were bred. On the other hand I never obtained this fly from *H. itala* which were collected in great numbers along the Grantchester Road.

(c) *Sarcophaga* sp. probably *S. crassimargo* Pand.[1]

There is not a single record in entomological literature of the life-history of this Sarcophagid.

I found its larvae last year in a few specimens of *H. virgata* collected from a large colony of these snails living on grass along a garden fence on the Barton Road, Cambridge.

The contents of the shells which harboured these larvae were reduced to a liquid putrefying mass, which, on a careful examination, showed also the chitinous remains of the mouth-parts, cuticle with spiracles, etc., of different stages of *Melinda* larvae. In one case, close to a *Sarcophaga* larva, I also found a recently killed larva of *M. cognata* which still contained all its internal organs.

All this shows clearly that the larva of *S. crassimargo* invades the snail which has been previously parasitised and killed by the larvae of *M. cognata* and that it then kills these larvae and lives upon the decomposed remains of their host.

The full-grown larva is 11 mm. long; it is composed of a pseudocephalon, three thoracic and eight abdominal segments, which bear numerous sinuous rows of small transparent and flattened hooks. The ventral side of the segments is covered with numerous hemispherical projections each bearing the sensory organs in the form of a pit surrounded by a ring of thickened chitin. The remains of the thoracic legs of the larva are represented by six groups of sensory organs each composed of three very short hairs. The respiratory system is amphipneustic. The prothoracic spiracles end in 15 papillae (Pl. XXV, fig. 22), the postabdominal, as is always the case in Sarcophagid larvae, lie in

[1] From the four pupae of this fly I obtained only one adult female. Unfortunately the females of *Sarcophaga* do not present very good characters for purposes of identification, though Mr Wainwright who examined this specimen found it to be almost certainly a ♀ of *S. crassimargo* Pand.

a deep posterior groove of the last (eighth) abdominal segment. The external chitinous ring which surrounds each spiracle (Pl. XXV, fig. 18) is not complete but interrupted near the scar (*sc.*). The three spiracular clefts are elongated and with their axes convergent towards this scar; the external openings of the perispiracular glands are exceedingly small.

The *Buccopharyngeal armature* (Pl. XXIV, fig. 11) is of the typical Cyclorhaphous form; the specific character here being the bilobed dorsal arm of the pharyngeal sclerite. All the other details of the structure of this organ are shown in the above mentioned figure.

The puparium of this fly can be easily recognised as belonging to a Sarcophagid by an examination of its posterior end which shows the spiracular pit. The prothoracic spiracles of the pupa are reduced to a pair of internal rosette-like organs which bear numerous papillae (Text-fig. 5) and which correspond to the internal spiracles of the *Melinda* pupa. The prothoracic spiracular horns, which in the latter protrude through the cuticle of the puparium, do not exist in this pupa nor in those of all the other Sarcophagids.

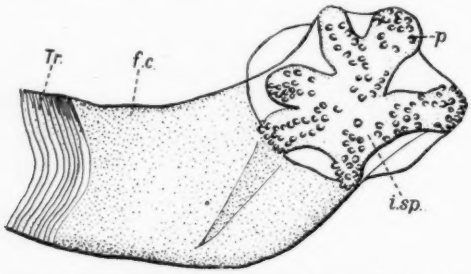

Fig. 5. Prothoracic spiracle of the pupa of *S. crassimargo* Pand. *f. c.* felt-chamber; *i. sp.* internal spiracle; *p.* spiracular papillae; *Tr.* tracheal trunks.

V. AN ACCOUNT OF ALL THE DIPTERA FEEDING UPON LIVING AND DEAD MOLLUSCS.

A great number of Diptera have been recorded living upon Molluscs, but our knowledge of the life-history of these insects is still very unequal. Whereas for a few of them we have a complete account of their development, for many others we only know that they were obtained from a particular species of Mollusc.

All these Diptera can be separated into four groups: (1) Parasitic, (2) Carnivorous, (3) Epizoïc, and (4) Saprophagous.

(1) Parasitic Forms.

The following species have been recorded as parasites of different snails:

Chironomus sp., the larvae of which were recorded by Barnard (1911) as living in the mantle cavity of *Limnea peregra* Müller, collected in the foun-

tain of Trafalgar Square (London). The larvae attack chiefly the young snails, which, when parasitised, usually leave the water. The author was not sure as to the real necessity of the Mollusc for the development of this Chironomid. This case of parasitism needs verification and more attention ought to be paid to the feeding habits of the larva and to its close relation to the host.

Melinda cognata Meigen.: the larvae live as parasites on *Patula rotundata* Müller and *Helicella virgata* da Costa. For the complete life-cycle of this fly see the first part of this paper.

Melinda sp., probably **Melinda gentilis,** is a parasite of *H. virgata* (see p. 442 of this paper).

Melanophora helicivora Goureau. Goureau (1843) obtained six specimens of this fly from seven specimens of *Helix conspurcata*, which he collected in Paris and enclosed in a paper cone. He concluded that the fly lays one egg in each shell, and that the larva which hatches from the egg devours the Mollusc and transforms itself into a pupa inside the shell of the host; the adult fly emerges in autumn. Goureau's observation, as I have already mentioned (1915*a*), is very incomplete and this case of parasitism also needs further verification.

It is somewhat interesting to mention here that the other species of this genus: *Melanophora roralis* L. was obtained by Heylaertes from *Asopia farinalis* (recorded by Van der Wulp 1869, pp. 184–185). Brues (1903), on the other hand, found the pupae of this species in an empty skin of *Porcellio* (terrestrial Isopod).

Some unidentified Dipterous larvae, living as parasites upon Molluscs, were recently recorded by Schmitz (1917). In two cases he found them in an *Arion* collected near Sittard, Holland, and in one case in a *Helix aspersa* L. collected in Luxemburg.

(2) CARNIVOROUS FORMS.

Mydaea sp. allied to **Mydaea bivittata** Macq. In a recent paper by Rodhain and Bequaert (1916, p. 248) we find the following observation on the feeding habit of the larvae of this Anthomyid:

"The genus *Mydaea* exists in central Africa and its larvae are carnivorous; one of us bred at Kivou a great number of a species allied to *M. bivittata* Macq. (identified by Dr Villeneuve) from the larvae devouring a big terrestrial Mollusc (*Burtoa nilotica* Pfeiff.)."

I would note that the larvae of the other species of this genus (*Mydaea ancilla* Meig., *urbana* Meig. and very likely *tincta* Zett. and *pertusa* Meig.) are either carnivorous, living upon the larvae of other Insects, or (*Mydaea pici* Macq., *anomala* Yaenn., *torquans* Nielsen and *spermophila* Townsend) producing subcutaneous myiasis in different birds.

(3) Epizoïc Forms.

Wandolleckia cooki Brues, a wingless Phorid fly discovered by Cook on a large terrestrial Mollusc from Liberia. According to Wandolleck (1898) these flies seem to feed upon the mucus of their host.

Wandolleckia biformis Schmitz, collected by Bequaert on a large Mollusc: *Achatina*, found in virgin forest, Belgian Congo.

According to Schmitz (1917), who described this fly, its development is similar to that of *Termitoxenia* as described by Wasmann (1900–1913), *i.e.* it has lost its larval and pupal stages and become *Ametabolic*, this loss being compensated for by a certain degree of development during the imaginal stage. As in *Termitoxenia*, Schmitz found also in this species two kinds of individuals: (1) stenogaster females with soft chitin and retracted abdomen and (2) physogaster, normally chitinised females, with well extended abdomen. The males are unknown, and Schmitz supposes this insect to be a protandric hermaphrodite.

In my previous paper (1915 *b*) I criticised the statement of Wasmann and insisted upon the fact that neither ametaboly nor hermaphroditism of *Termitoxenia* and *Termitomyia* is yet proved. To what is mentioned in my paper I can now add that the existence of steno- and physogaster forms does not demonstrate the ametaboly of an insect; in fact these forms are known in *Puliciphora pusillima* de Meijere (1912, Pl. IV, figs. 16 *a* and 16 *b*) while in another species of the same genus, *P. beckeri* de Meijere, both larval and pupal stages have been described and figured by de Meijere.

As to the protandric hermaphroditism of these insects, the only way to prove its existence is to find in the stenogaster forms all the stages of spermatogenesis, *i.e.* the spermatogonia and spermatids.

(4) Saprophagous larvae and doubtful parasites.

In this group, besides Phorids and several Acalypterates, we shall place Sarcophagids, though for a few of these flies the records are still contradictory and there is even a tendency to consider them as true parasites.

As on the other hand the complete life-history of these Sarcophagids is still unknown it is better to consider them as doubtful parasites and to examine them with the saprophagous forms.

SARCOPHAGIDAE.

Sarcophaga carnaria L. According to Portchinsky (1887, p. 17) a great number of these flies, which he identified as *S. atropos* Meig. (= *S. carnaria* L.), emerged from a lot of *Helix stavropolitana* collected by König in the Caucasus. König mentioned that the larvae had apparently no effect upon the life of the snails, which lived in captivity a long time after the appearance of the flies.

This observation does not seem to be complete, and very likely the Sarcophagids hatched from pupae enclosed in some dead snails which he probably overlooked since he was dealing with a great number of these animals.

Mik (1890, p. 153) stated that this *Sarcophaga* was obtained by Brischke from another Mollusc: *Succinea* sp. We know also that the larvae of this common and well known species have often been recorded from wounds and from the cavities of the mouth, nose, ears, etc., of different mammals.

Sarcophaga sp. probably *S. crassimargo* Pand. The larvae of this species live upon dead *Helicella virgata* da Costa previously killed by *Melinda cognata* Meig. (see p. 443 of this paper).

Sarcophaga haemorrhoa Meigen. According to Mik (1890, p. 153) this species was bred by Prof. Bertkau of Bonn, from a *Helix hortensis* found attached to a leaf and which he supposed to be still alive. Schmitz (1917, pp. 25–27) obtained this fly from a young *Helix* (*nemoralis* or *hortensis*) collected in a wood near Maastricht.

Sarcophaga helicis Townsend. The first record regarding the life-history of this Sarcophagid is found in an interesting note by Townsend (1892, pp. 220-221) the main part of which I reproduce here:

"I have recently received from Mr H. A. Surface, of the Ohio Experiment Station, a small Sarcophagid which he bred from *Helix thyroides* Say, while engaged on his catalogue of shells of Franklin County, published in Bulletin 2, Vol. 1, technical series, of that station.

Mr Surface accompanies the specimen with the following note: 'The snail was placed in a tight bottle August 25, in Warren County, Ohio, and during the first part of September the pupae were seen. From September 27 to 30 five or six mature flies came forth.' The fly proves to be a small species of Sarcophaga. After considerable time spent in looking over descriptions of North American species, I felt justified in considering it new."

According to Aldrich (1916, pp. 158–161) this species is one of the commonest North American Sarcophagids, and was bred from different Insects. Numerous records of the life-history of this species were mentioned by Aldrich in his note on "The economic relations of the Sarcophagidae" (1915) and in the above quoted monograph on the "Sarcophaga and allies."

I will quote here the following passage from the latter monograph (p. 160): "It is very likely that the species breeds largely in dead insects, and some of the records were made without allowing for this possibility. However, the species is a true parasite in grasshoppers and in *Eleodes*, and probably quite often in Lepidoptera and other insects. With this element of uncertainty to be kept in mind, the following are the cases of rearing recorded for the material I have examined." He then gives a full report on these cases, from which it is only necessary to mention that this fly was recorded from adult *Corydalis cornuta*, *Cicada tibicen*, *Calosoma* sp., *Leucania unipuncta*, adult *Lachnosterna*

arcuata, adult beetle *Dinapate wrightii*, from grasshoppers, larvae of Army Worm, from *Eleodes opaca* and finally from a Myriapod: *Sparabolus* sp.

Sarcophaga nigriventris Meigen, obtained by Giard (see Böttcher, 1913, p. 367) from *Helix cantioniformis* by Bowell (1917) from *Helicella itala*, and by me from *Helicella virgata* da Costa and *H. cantiana* Montagu (see pp. 442–443 of this paper).

Sarcophaga noverca Rond. bred by Schmitz (1917, p. 30) from a *Helix* found in Maastricht.

Sarcophaga privigna Rond. According to Mead (1897, p. 251), J. Künckel d'Herculais obtained this Sarcophagid from a *Helix lactea* from Algeria.

Sarcophaga setipennis Rond. bred by A. Giard (see Böttcher, 1913, p. 367) from *Helix acuta*, collected near Wimereux, Pas-de-Calais and by Schmitz (1917, p. 30) from an empty shell of a snail collected near Zaragoza, Spain. The adult fly was also recorded by this author from near Sittard, Holland.

Sarcophaga teretirostris Pand. obtained by me from a dead specimen of *Helicella cantiana* Montagu.

Sarcophaga sp. I found a few larvae of an unidentified Sarcophagid in dead *Helix aspersa* collected near Paris and in *Helicella cantiana* collected in Cambridge.

Helicobosca muscaria Meigen. The larvae of this fly were discovered by Perris (1850, pp. 119–122) in the snails *Helix pisana* Müll. collected in France near Mont-Marsan (Landres). He never found more than one larva in each snail. Before it pupates, the larva usually leaves the shell and burrows into the earth, but in some cases the pupae are formed in the snails. Perris supposed that the larvae feed only upon the dead Molluscs. In his paper he gives a description and figures of this larva. More recently, Schmitz (1910, pp. 107–109, 1917, p. 27) gave a complete account of the life-history of this fly. He found that the female deposits a big larva, about 5 mm. long, in a dead snail, about every 14 days; four or five weeks later this larva pupates and in this stage the insect hibernates, the adult emerging in the following spring. This low productive capacity of the fly and the long duration of the life-cycle explain according to Schmitz the rarity of this insect.

The internal genital organs and their function were described by Cholodkovsky (1908) and the mouth-parts of the first-stage larva by Nielsen (1917).

ANTHOMYIDAE.

Homalomyia canicularis L. I have bred this fly many times from different dead snails: *Helix pomatia*, *aspersa*, *nemoralis* and *hortensis* (see Keilin, 1911, p. 30). On the other hand the larvae are very common in all kinds of decomposed organic matter; they prefer however matter containing much ammonia,

and continue to live therein when all other dipterous larvae either depart or are killed in it.

PHORIDAE.

Aphiochaeta rufipes Meigen. The larvae of this fly were found by me in very great numbers, and in different places, living in dead snails: *H. pomatia*, *aspersa*, *nemoralis* and *hortensis*. My previous paper (1911, pp. 61–75) gives an account of its complete life-history and a description of the larval and pupal stages. The larvae of this species have also been recorded from different decomposed organic substances.

Aphiochaeta ruficornis Meigen. I have obtained the larvae of this fly only by killing snails and allowing them to putrefy. The material was obtained in Paris in the garden of the "École Normale Supérieure." For a complete description of the different stages of this insect see my previous paper (1911, pp. 76–78).

Phora bergenstammi Mik. According to Mik (1864, p. 793) this fly was obtained by von Bergenstamm from pupae found in a shell of *Helix pomatia*. In 1908 and 1910 Schmitz recorded the pupae of this insect from different snails. In 1911 I gave a complete description of the life-history and larval morphology of this fly (pp. 31–56) which I bred from different dead snails: *H. pomatia*, *aspersa*, *nemoralis*, *hortensis* and *arbustorum*.

Phora bohemani Becker. Schmitz (1908, 1910, 1917) found the pupae of this fly in different dead snails.

Phora immaculata Strobl, bred by Schmitz (1917, p. 36) from dead snails; there are two generations per annum. The pupa resembles that of *Ph. bergenstammi* Mik.

Phora maculata Meigen. The pupae of this species were found by Dufour (1840) in a shell of *H. aspersa*. Schmitz (1908, 1910, 1917) recorded them from the shells of different snails. To this species belongs also the puparium which I described as *Phora* No. 1 (1911, pp. 57–60). In 1912 my late friend J. Bonnet sent me a great number of dead snails: *H. aspersa* and *nemoralis*, collected by him near Toulouse, France, which contained the larvae and pupae of *Ph. maculata* Meig. (Text-fig. 6.)

Phora pressata Becker. In a few *Helix nemoralis* collected at Chaville, near Paris, I found the pupae which by breeding gave a *Phora* described by M. Becker as *Phora pressata* n.sp. In 1912 M. Becker proposed that I should insert his description of this species in the second part of a paper on the life-history of different Phorids. Circumstances prevented me from finishing this investigation and I therefore give now the description as it was sent to me in 1912.

Phora pressata n.sp. ♂ ♀.—

Rufa, thoracis dorso vix nitente, pilis nigris, setis dorsocentralibus duabus;

scutelli margine setis duabus; halteribus flavis.—Frons lata nigra opaca; antennis mediocribus fulvis, arista vix pubescente, palpis flavis.—Abdomen nigrum opacum, secundo et sexto segmentis longioribus, anguste niveo-marginalis.—Pedes toti flavi, femoribus posticis dilatatis; tibiis anticis antice unispinosis; tibiis mediis antice et apice unispinosis; tibiis posticis in medio et apice bispinosis.—Alae fere hyalinae, margine antico setulis brevibus.—Longit. corp. 2 mm. Patria: Gallia.

Affinis Phorae unicalcaratae Beck et erythronotae Strobl.

Phora unispinosa Zett. I found the larvae and pupae of this insect in dead *H. aspersa* picked up in the garden of the "École Normale Supérieure" of Paris. Their life-history is similar to that of *Phora bergenstammi* Mik.

Fig. 6. A shell of *Helix aspersa* with the upper whorl broken, showing the pupae of *Phora maculata* Meigen fixed to the inner side of the shell.

Phora sp. No. 2. Under this name I described the empty pupae (1911, p. 60) of a Phorid found in one specimen of *H. nemoralis* collected in Bernese Oberland, Switzerland.

Phora sp. the pupae of which were recorded by Schmitz (1917, p. 39) from a shell of a species of Pupid mollusc collected near Lisbon.

Hypocera molluscivora Schmitz, **Dorniphora bequaerti** Schmitz and **Pulicophora spinicollis** Schmitz, according to Schmitz (1917), were bred by Bequaert with **Aphiochaeta xanthina** Speiser from different Molluscs (probably bivalves) from Africa.

EPHYDRIDAE.

Discomyza incurva Fallen. The larvae of this fly were found by von Bergenstamm (1864) in a dead *H. pomatia*. The pupae are fixed inside the shell in the same way as those of *Phora bergenstammi* Mik. I found near Paris one shell of *H. pomatia* containing a few of these pupae.

SCIOMYZIDAE.

Ditaenia cinerella Fallen, obtained by Schmitz (1917) from a shell of a *Helix* collected near Zaragoza, Spain.

Salticella fasciata Meigen. Perris (1850, pp. 122–123) found the larvae in a dead *Helix pisana*. According to Schmitz (1917, p. 29) it is not yet proved whether they are parasites or saprophagous larvae.

DRYOMYZIDAE.

Dryomyza sp. Schmitz recorded this fly as a not very common inhabitant of dead snails.

SEPSIDAE.

Nemopoda cylindrica Fabricius, bred by me from the larvae found in different dead snails. The eggs are of a peculiar shape having a very long filiform peduncle. These larvae occur also in the excrement of different domestic animals.

BORBORIDAE.

Borborus, Sphaerocera and **Limosina** have been recorded by Schmitz (1917, p. 30) from dead snails, but they occur also in all kinds of decomposed organic substances and especially in manure.

PSYCHODIDAE.

Philosepedon phalaenoides L. I have often found the larvae and pupae of this species in different species of decomposed snails (see Keilin, 1911, p. 30).

Philosepedon humeralis Meigen was recorded in dead snails by Westwood, Verrall, and recently by Schmitz (1917) who bred this insect from snails collected in Lisbon, Zaragoza and Maastricht.

APPENDIX.

OBSERVATIONS OF M. E. SÉGUY ON *MUSCA DOMESTICA* LARVAE DEVOURING LIVING SNAILS.

On 24. iii. 1919 I received from M. E. Séguy of Rambouillet, France, a letter in which he communicated several of his unpublished observations bearing upon the relation between the house-fly and snails. The following is a summary of his letter:

He collected several snails, having the shell closed by the epiphragm, and examined them, breaking the latter, in the hope of finding the Phorid larvae. The snails secreted another epiphragm, but ten days later they were destroyed by the larvae of *Musca domestica*.

Living snails, closed with epiphragms, were put in a jar containing the larvae of *M. domestica*. In eight days the snails were completely eaten up by the larvae. The latter burrowed their way through the epiphragm and completely penetrated into the foot of the Mollusc. The penetration occupied about eight hours, and the abundant secretion of mucus by the snail did not seem to disturb the larva. The attacked snails are very often covered with a mite: *Eyrenetes limaceum* Schrank. The larvae, after they have destroyed one snail, pass easily into another living or dead specimen.

Living snails were placed under a bell-jar containing several pairs of *M. domestica* and 12 days later they were all devoured by the maggots. In the middle of January, 50 snails were collected from the wall close to the military hospital, they were separated in tightly closed jars which were placed at 25° C., 9 of the 50 Molluscs yielded *M. domestica* larvae.

The larvae, pupae and adults of this fly, bred from the snail, seem to be smaller than those which live or are bred from decomposed organic substances.

Séguy also recorded the presence in the snails of the larvae of *Calliphora erythrocephala* and *Phora giraudii* Egg.

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EXPLANATION OF PLATES XXII—XXV.

PLATE XXII.

Male (1) and Female (2) of *Melinda cognata* Meigen. ×8.

PLATE XXIII.

(The surface structure of the snail's skin is schematized in Figs. 1 and 3.)

Fig. 1. *Helicella* (*Heliomanes*) *virgata* da Costa, with the anterior part of its body extracted from the shell and with opened mantle cavity (*m.c.*) showing a big second stage larva (*L.*) of *Melinda cognata* Meigen. The larva has been cleared from the distended integument of the kidney which partly covered its body. The dissecting needle (*a*) points the position of the pneumostome of the host towards which are directed the postabdominal spiracles of the larva.

Fig. 2. An empty shell of a young specimen of *H. virgata* with two larvae of *Melinda cognata*; *sp.*, spiracles. One of these larvae developed in this shell, the second migrated thither from another shell as the insects frequently do before pupation. ×8.

Fig. 3. A young *H. virgata* extracted from its shell and showing by transparency in its mantle cavity (*m.c.*) an egg (*ov.*) of *M. cognata*, and, in the kidney (*k.*) a first stage larva (*L.*) of this fly. The posterior end of the larva, bearing the spiracles, protrudes into the mantle cavity of the host; *liv.*, liver. The same specimen contains also the crumpled chorion of an empty egg belonging to the first stage larva.

Fig. 4. Egg of *Melinda cognata* (*a*) and the structure of its surface (*b*). *a* ×42, *b* ×240.

Fig. 5. Puparium of *M. cognata* from dorsal side, showing the respiratory horns (*h.*). ×8.

Fig. 6. *H. virgata*, retracted in its shell and showing the posterior end with spiracles of the third stage larva of *M. cognata*, protruding from the pneumostome of the host; *f.*, foot of the snail. ×6.

PLATE XXIV.

All the figures are of the buccopharyngeal armatures of different larvae viewed laterally.

Letters common to these figures: *an.*, antennae; *b.scl.*, basal or pharyngeal sclerite; *int.*, intermediate sclerite; *lbm.*, labium; *Lbr.*, labrum; *l.h.*, lateral hooks; *l.e.*, lateral emargination; *m.p.*, maxillary palps; *ph.*, pharynx; *s.d.*, salivary duct; *s.e.*, supplementary emargination; *t.*, triangular plate.

Fig. 7. Head and buccopharyngeal armature of the first stage larva of *M. cognata*. ×240.

Fig. 8. Buccopharyngeal armature of the first stage larva of *Melinda* sp. probably *Melinda gentilis*. ×240.

Fig. 9. The same organ of the third stage larva of *M. cognata*. ×84.

Fig. 10. The same organ of the second stage larva of *M. cognata*. ×240.

Fig. 11. Buccopharyngeal armature of the third stage larva of *Sarcophaga* sp. probably *S. crassimargo*. ×42.

Fig. 12. The same organ of the first stage larva of *Pollenia rudis* Fab. parasite of earthworm (*Allolobophora chlorotica* Sav.).

Fig. 13. The same organ of the first stage larva of *Onesia* sp. probably *Onesia vespillo*.

PLATE XXV.

Letters common to all the figures of this plate: *a.g.*, accessory glands; *c.*, anterior intestinal coeca; *d.n.*, dorsal central nervous system; *f.c.*, felt chamber of spiracles; *i.d.*, imaginal discs of the head; *i.sp.*, internal spiracles of the pupa; *m.g.*, midgut; *o.*, external opening of perispiracular glands; *od.*, oviduct; *oe.*, oesophagous; *ov.*, ovary; *p.*, spiracular papillae; *per.*, peritrems of spiracles; *ph.*, pharynx; *pr.*, proventriculus; *rec.*, rectum; *r.h.*, respiratory horn of the pupa;

r.s., receptacula seminis; *s.c.*, external spiracular scar; *s.d.*, salivary duct; *s.gl.*, salivary gland; *Tr.*, tracheal trunks; *ut.*, uterus; *v.n.*, ventral nervous system.

All the figures except figs. 18 and 22 concern *Melinda cognata*.

Fig. 14. Dissection of the anterior portion of the third-stage larva of *M. cognata* Meig.

Fig. 15. Anterior prothoracic spiracle of the second-stage larva, with four papillae. × 240.

Fig. 16. Internal genital organs of a female emerged from the pupa August 15th, kept in laboratory on sugar and honey and dissected November 5th. × 16.

Fig. 17. Prothoracic spiracle of the second-stage larva, with six papillae. × 240.

Fig. 18. Postabdominal spiracles of the third-stage larva of *Sarcophaga* sp. probably *S. crassimargo*. × 84.

Fig. 19. Prothoracic horns with internal spiracle of the pupa of *M. cognata*. × 134.

Fig. 20. Postabdominal spiracle of the third-stage larva of *M. cognata*. × 240.

Fig. 21. A similar spiracle but of abnormal structure, with one peritreme reduced. × 240.

Fig. 22. Prothoracic spiracle of the third-stage larva of *Sarcophaga* sp. probably *S. crassimargo*. × 84.

Fig. 23. Postabdominal spiracle of the second-stage larva of *M. cognata*. × 240.

Fig. 24. A similar postabdominal spiracle but of abnormal structure. × 240.

Fig. 25. Prothoracic spiracle of the second-stage larva of *M. cognata*, with five papillae. × 240.

Fig. 26. Prothoracic spiracle of the third-stage larva of *M. cognata*. × 240.

THE ANATOMY OF THE HEAD AND MOUTH PARTS OF *PSYLLA MALI*, THE APPLE SUCKER, WITH SOME REMARKS ON THE FUNCTION OF THE LABIUM.

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(With Plates XXVI—XXVIII and one Text-figure.)

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INTRODUCTION.

The investigation, of which the results contained in this paper are a part, was first commenced in 1910. It was then proposed to describe in some detail the entire anatomy of the adult insect, but when a measure of progress had been

made, and the alimentary, tracheal, and nervous systems had been almost completed, the work was interrupted by my taking up an appointment in India. On returning to England in 1915, the enquiry was resumed for a short period at the end of the year, but early in 1916 it had to be abandoned again to meet the superior claims of entomological work with the Forces in Mesopotamia, for the War Office. This, and other investigations connected with problems which have arisen in England in consequence of the War, prevented any further progress being made, but, with the declaration of the Armistice it was felt that attention might once more be given to it. In the limited time which could be devoted to the work, it has not been possible to carry out the original plan of including the whole anatomy in one paper, and the description of the head and mouth parts has been selected because of the somewhat novel considerations which have arisen in connection with the latter, particularly with regard to the function of the labium during the operation of piercing, the publication of which it seemed undesirable to delay further.

The initial stages of the work were assisted by a grant from the Endowment of Research Fund of the Birmingham Natural History and Philosophical Society, for which I wish to express my thanks to the Trustees; and I am also much indebted to Professor F. W. Gamble, F.R.S. for help and advice.

METHOD.

The material used was obtained from apple orchards around Redditch. The fixative which was found to give the best results was a very hot solution of picro-sulphuric acid according to the following formula:

Distilled water	100 c.c.
Sulphuric acid	2 c.c.
Picric acid to saturation.	

Other fixatives, such as Petrunkewich's modification of Gilson's fluid, were tried, but were not so successful. An additional advantage of the picro-sulphuric solution is that the chitin takes up the picric acid strongly so that it appears in the sections stained a deep yellow colour which renders the chitinous parts easily distinguishable. The usual series of transverse, longitudinal horizontal, and longitudinal vertical sections were prepared, and stained with Erlich's haematoxylin. In addition to the serial sections, dissections and preparations of the chitinous parts of the head were made, after treatment with caustic potash. The figures were all drawn from the sections or preparations by means of the Camera Lucida.

NOMENCLATURE.

During recent years, considerable discussion has arisen regarding the homologies of the cephalic skeleton and mouth parts of Hemiptera. The progress of the controversy has been summarised by Awati (1914) and Davidson (1914) so that there is no necessity to give a further summary here in detail,

but in order to avoid any confusion with regard to the significance of the terms used in the body of the paper, it will be useful to indicate here the meaning ascribed to them and the reasons for adopting them. Of the two main questions indicated above, that connected with the homology of the setae in the Hemiptera, has perhaps been more definitely solved. Muir and Kershaw (1911–1912) by their researches into the embryology of *Pristhesancus papuensis* and *Siphanta* have shown that in both Homoptera and Heteroptera the anterior setae represent the mandibles, and the maxillary plates and the posterior setae together, represent the maxillae. The anterior setae, which owing to the extreme depression of the head in *P. mali*, have come to occupy a ventral position, will therefore be termed the mandibles (or mandibular setae) and the posterior setae, the maxillary setae.

The homologies of the sclerites which go to the formation of the head capsule, and which surround the buccal cavity, cannot be dismissed so easily. It is not intended here to enter into the discussion, but it is evident from what has been found in *P. mali*, which exhibits some special and probably advanced features, that the problem can only be solved by a wider survey of the different types of head found within the order than has already been made. The formation of the dorsal portion of the head presents little difficulty. This is usually termed the epicranium, a useful term when speaking of this portion as a whole, but Crawford (1914) states that in the Psyllidae this portion of the head is formed by two sclerites, the *vertex* and *occiput*, and that in some cases the latter contributes largely to the formation of the side of the head. These terms will therefore be adopted, the *vertex* forming the region between the eyes, and the *occiput*, the narrow posterior region of the head, where it articulates dorsally with the neck. When the sclerites which surround the mouth parts are considered, it is evident that some confusion both as regards homologies and nomenclature prevails. Muir and Kershaw (1911*a*) endeavoured to show that the mouth parts were homologous throughout the Homoptera and Heteroptera and figured nine examples of which three belonged to the Homoptera and six to the Heteroptera. On their interpretation the buccal region is made up of the clypeus, which has two lateral sclerites (these apparently alternatively termed the lorae, and corresponding to the mandibular sclerites of Meek), the labrum and the epipharynx; and the latero-ventral portion of the head is formed by the maxillary plates which are, judging from the figures, continuous with the genae above, but show no articulating suture. (In a later paper (1911*b*) the authors describe these maxillary plates as completely amalgamated with the head capsule and leaving no suture.) The fundamental point upon which the authors base their interpretation, is the articulation of the mandible with the head capsule. In the attempt to apply their results to *P. mali* difficulties at once arise, for in this insect the mandible has no skeletal articulation with the sclerites of the head. The extent to which the head has been deflexed has also resulted in modifications of the arrangements of the parts in the buccal region, and possibly in the reduction of some

of the sclerites. Unfortunately, Muir and Kershaw do not give the relation of the parts to one another as they would appear in section (except in one case, *Flata*, in which the arrangement of the sclerites is quite different from that in *P. mali*), but only the outward aspect—which, from the configuration of the head, is very difficult to investigate in *P. mali*—so that correlation of the parts by general comparison is difficult. Previous writers on the anatomy of the head of the Psyllidae show no unanimity of nomenclature. Witlaczil (1885) confines himself to very general terms and does not differentiate the sclerites of the head beyond distinguishing the "Vorderkopf" or forehead which includes those median sclerites which—from its deflexed condition—lie on the ventral side of the head. Stough (1910) states that the head is enclosed by the epicranium, genae and frontal cones together with the antennal sockets and compound eyes and ocelli, and that the mouth parts are composed of the labrum, epipharynx, labium, hypopharynx and setae, and closely associated with them, the frons, clypeus, mandibular and maxillary sclerites (after Meek) and the tentorium. This interpretation is criticised by Crawford (1914), who points out that Stough has overlooked the frons proper, calling it the ligamentary process of the frons, and consequently has misnamed the clypeus proper as the frons, and introduced an extra suture into the clypeus so that the correct number of sclerites appear to be present. On Crawford's interpretation—which is arrived at from a review of a large number of species—the lower portion of the head in the Psyllidae is made up of the following sclerites: the *frons*, a very variable and in many instances small sclerite which joins on to the vertex between the genae, and carries the median ocellus; the *genae*, which form the portion of the side of the head which lies between the vertex and clypeus, and from which project the *genal cones*, two lobes or conical processes, which project downwards from the head, and obscure the "face" proper; the *clypeus*, a relatively large and prominent sclerite, immediately ventral to the frons, and which converges rapidly towards the *labrum*, which is relatively short, and terminates in an inconspicuous *epipharynx*. Among the appendages of the head, the author includes the *labium* which is three-jointed and sharply flexed, the *mandibular* and *maxillary setae*, the *eyes*, and *antennae*. It will be seen that the author makes no mention of the maxillary plates of Muir and Kershaw, nor of the lateral sclerites (lorae) to the clypeus, but it is evident that he is dealing only with those sclerites which are clearly visible from the exterior. Without therefore elaborating the discussion further, which, as indicated above, would necessitate a wide survey of a large number of types to solve satisfactorily, it must suffice to state that in this paper the terms frons, clypeus, labrum, gena, etc., are used in the way indicated by Crawford. The term maxillary sclerite is used in the paper to denote a structure which appears to correspond to the maxillary plate of Muir and Kershaw, but since the structure is not exactly a plate, the term sclerite has been adopted as being more appropriate.

THE EXOSKELETON OF THE HEAD.

The Head Capsule.

The head of *P. mali* is of the usual psylline type. It is somewhat flattened in appearance, antero-posteriorly, is wide between the eyes, and the depression of the head so commonly met with in the Homoptera, is carried to extreme limits, so that the buccal region and the oral appendages extend backwards between the coxae of the first pair of legs. Consequently, the labium appears as if it arose from the prosternum. The front of the upper portion of the head is formed by the vertex, a quadrate sclerite with a strongly marked median suture. The compound eyes are attached to the lateral margins of the vertex. The frons is very small and is almost hidden from view by the genal cones which arise from the ventral margin of the vertex and project downwards in front of the head almost obscuring the facial portion. The antennae are articulated to the head just below the eyes, between the lateral margins of the vertex and the genal cones. The front of the head or the "face" proper, which from the deflexed condition of the head occupies a ventral position, is formed by the clypeus and labrum. The clypeus is a domed, pyriform sclerite attached at its upper broad end to the frons, and gradually tapering off into the labrum, which terminates in a comparatively insignificant epipharynx. The side of the head is formed by the gena, a sclerite, the posterior margin of which is not very clearly defined, but soon becomes involved with the episternite and coxa of the prothorax, and shades off almost imperceptibly into the conjunctival membrane connecting it with the prothorax. The gena is continuous along its anterior margin, with the under side of the genal cones, of which the latter are really protuberances. The articulation of the head, above, with the thorax is effected by the junction of the lower margin of the occiput with the flexible membrane of the neck. The occiput is a long narrow sclerite stretching between the posterior margins of the eyes and forms the back of the upper portion of the head.

The Buccal Region and Labium (Plate XXVII).

Owing to the extreme depression of the head, the whole of the oral region lies buried between the coxae of the first pair of legs, so that the relation of the sclerites which form the boundaries of the buccal cavity cannot be readily distinguished from the exterior (Pl. XXVIII, fig. 1). This can therefore be best described by considering a series of transverse sections of the head. After the region of the frons has been passed, the clypeus appears forming the ventral wall of the head, and, owing to its domed character it appears semicircular in outline (Pl. XXVI, fig. 2). Its lateral margins are carried to some distance into the head, where they become continuous with the incurved ventral margins of the genae, which form the sides of the head. Thus at the junction of these sclerites, a groove—the clypeal groove—is formed in the surface of the face.

As the sections are traced backwards, it is seen that in the region of the bases of the setae, two hollow, flattened, strongly chitinised structures appear just dorsal to the setae and between the maxillary setae and the nervous system. These structures are the buccal folds (Pl. XXVI, fig. 4). As the buccal region is approached, the buccal folds extend inwards towards the median line until in the region of the termination of the pharynx, the innermost wall of each fold gradually approaches and eventually becomes continuous with the strongly chitinous posterior wall of the pharynx. In the meantime, the clypeal groove has become deeper, and in the region of the commencement of the labrum-epipharynx, the closed end of the groove bifurcates so that in section the groove has now taken the form of a Y. The stem of the Y represents the old clypeal groove, and at its base the cavity is open to the exterior. The inner arm of the Y extends upwards into the head in the direction of the pharynx, and the outer arm towards the outer edge of the buccal fold. Eventually these various structures become continuous with one another. The innermost wall of the inner arm of the Y joins on to the end of the ventrally directed arm, of its side, of the Λ-shaped posterior wall of the pharynx. The outer wall of the inner arm of the Y becomes continuous with the inner margin of the ventral wall of the buccal fold. The inner wall of the outer arm of the Y fuses with the outer margin of the ventral wall of the buccal fold, and the outermost wall of the outer arm with the lateral margin of the dorsal wall of the buccal fold. The total result of this anastomosis is the formation of the buccal cavity and maxillary sclerites (Pl. XXVI, fig. 5), and the differentiation of the hypopharynx and epipharynx. The buccal cavity takes in section the shape of an inverted triangle with an incompleted apex (▽) and lies buried between the anterior portions of the coxae of the first pair of legs. The space between the incompleted sides of the ▽ is filled by the epipharynx, which is formed by the fusion of the labrum with the ventral or anterior wall of the pharynx. The middle portion of the base of the ▽ is occupied by the hypopharynx, which arises, as indicated above, by the fusion of the inner margins of the buccal folds with the posterior wall of the pharynx. The remainder of the cavity is occupied by the maxillary sclerites, which lie one on either side of the epipharynx, and in section take the form of scalene triangles with their shortest sides applied to the dorsal surface of the buccal cavity.

The setae, as they pass out from the head, enter the buccal folds and are received into furrows on the inner sides of the maxillary sclerites. Continuing backwards, it will be seen that when the hypopharynx has been passed, the upper margins of the maxillary sclerites approach one another in the median plane until they meet over the top of the epipharynx. At this point the upper portions of the maxillary sclerites are so shaped that they fit into one another and interlock (text-fig. 1). Also, the ventrally directed portions of the sclerites embrace the epipharynx and fit into grooves on the sides of that organ, with the result that these three structures fit closely together in a manner similar to that of the pieces in a jig-saw puzzle.

In the region where the dorsal surface of the epipharynx is applied to the ventral wall of the inner portions of the maxillary sclerites, a system of ridges and grooves appears on the approximating surfaces, so that when the parts are applied to one another, three channels are formed; a larger median one with two smaller ones, one on each side (text-fig. 1). The median channel receives the maxillary setae and each outer channel a mandible. Eventually the maxillary sclerites lose their triangular shape in cross section and become flattened against the dorsal wall of the buccal cavity, but the epipharynx which is now reduced in size is still applied to their under surfaces (Pl. XXVII, figs. 2–3).

By this time, a deep groove or fold has appeared in the centre of the dorsal wall of the buccal cavity, and as the sections are traced backwards, it will be seen that this groove, shallow at first, passes into a deeper fold in the ventral wall of the body between the coxae of the first pair of legs (Pl. XXVII, figs. 4–6). This groove or fold extends upwards into the body and actually pierces the nervous system which, in this region, assumes the form of two cords one of which, in the sections, lies on each side of the groove. The cavity or lumen of this groove forms a chamber in which a loop of the setae lies when they are not in use, and consequently an appropriate name for this structure will be the *setal chamber*.

These structures have not been described in detail by previous writers on the anatomy of the Psyllidae. Witlaczil (1885) indicates the presence of the setal chamber. He says (p. 603):

"Die Stechborsten, welche in einer Rinne der Unterlippe liegen, und am Ende derselben heraustreten, sind hier aber so lang, dass sie an der Basis der Unterlippe eine Schlinge bilden, welche in einem Hautsacke liegt, der durch eine Einstulpung der Hypodermis gebildet wird und das Centralnervensystem an der Grenze von Unterschlundganglion und Bauchmark durchbohrt."

This author also indicates that a similar structure has been described by Dujardin and Mark in the Coccidae. Stough (1910) draws attention to the similarity between the psyllid and coccid mouth parts, and says that in the latter "the setae are retracted into a special pouch when not in use." He then dismisses the subject by stating: "The parts exclusive of the labium are similar in general structure to the same parts in *Pachypsylla*." Crawford (1914) does not mention any special structure for accommodating the loop of the setae, although in one of his figures (Pl. XXVIII, fig. 15) he shows that the setae describe this loop before entering the labium.

To return to the consideration of the serial sections of the head; in the region where the setal chamber has become clearly distinguishable, it is seen that the configuration of the surrounding parts has now altered. The maxillary sclerites have completely disappeared and only the tip of the epipharynx remains (Pl. XXVII, fig. 4). The buccal cavity too has become almost obliterated, but the setae still remain at the buccal end of the setal chamber. Further back still, the region of the buccal cavity proper has now been passed, and the

groove of the setal chamber is more strongly developed. A fold or furrow has now appeared in the chitin of the body wall a little to each side of the setal chamber and dorsal to the coxae of the first pair of legs (Pl. XXVII, fig. 5). These folds, as they are traced backwards, curve more and more upwards and inwards towards the median line so that there are formed two short, almost cylindrical, sclerites which lie one on either side of the setal chamber and are fused to the body of the insect along their dorsal margins (Pl. XXVII, figs. 6–7). If these structures are traced further back still, it will be seen that they become continuous with the free portion of the labium or proboscis, the upper portion of which lies in a groove or furrow—the labial furrow—between the procoxae. The inner margins of this furrow are formed by the furcae from the prothorax which are described by Crawford (1914) as embracing the labium. The relation of the parts to one another in this region, throws some light upon the homologies of the setal chamber, for it is evident that the cylindrical sclerites which have been indicated above as lying one on each side of the open base of the setal chamber are clearly portions of the first joint of the labium, and as the setal chamber passes right through this joint, and at its posterior margin becomes continuous with the groove on the anterior face of the free portion of the labium, it can be concluded that the setal chamber is an extension of the labial groove.

The labium in the Psyllidae, as already shown by Witlaczil (1885), Stough (1910) and Crawford (1914), consists of three joints or segments. As has been indicated above, the first joint is fused for a great part of its length with the body, and is divided longitudinally to give access to the setal chamber. The free portion of the labium (Pl. XXVIII, fig. 2) is therefore made up of the second and third joints, and projects almost vertically downwards from the body, but is hidden from view by the proximal joints of the first pair of legs. The second joint is the longest, its walls are but thinly chitinised, and at its distal end it becomes bulged or expanded on its anterior face. The third, or terminal joint is much shorter and smaller in diameter and tapers off at the end. The termination of the joint is furnished with a number of stiff tactile hairs. As a result of the fusion of the proximal portion of the first joint with the body, the labium does not trace a straight course, but is sharply flexed at the junction of the first and second joints. The labium varies, both in cross section and in the character of the groove which runs along its anterior face, from its proximal to its distal portion. In the region where it just becomes free, that is, at the junction of the first and second segments, it is flattened in cross section, and the groove, which is not strongly developed, lies at the bottom of a V-shaped depression in the anterior face of the organ. By the time the middle portion of the second joint is reached, the organ has become almost triangular in section and the groove, which is now heavily chitinised, has become enclosed within the body of the labium. This is effected by the gradual approximation of the sides of the V-shaped depression referred to above, so that now the groove containing the setae appears as an expansion of the closed end of a

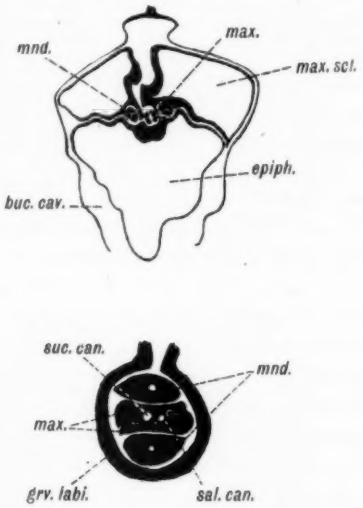
deep parallel-walled channel, which opens out on the front face of the labium. Within the terminal joint, this channel becomes relatively shallower following upon the reduction of the diameter of the segment, and at the tip the groove containing the setae, in addition to becoming contracted, is considerably strengthened by reason of the added thickness of its walls. As a consequence of this, the setae are firmly enclosed so that in some preparations in which, from the treatment to which they have been subjected, the upper parts of the setae have become displaced from the groove, the terminal portions will still remain securely retained in position within the tip of the proboscis.

The Setae.

The setae of *P. mali* are of the usual Homopterous type. They are four in number, arranged in pairs, one pair being anterior to the other. As has been indicated in the first part of this paper, the homologies of the Hemipterous setae are now generally accepted, so that it may be taken that the anterior pair are the mandibles, and the posterior pair the maxillary setae. Each seta consists of a hollow, conical, expanded basal portion within which is to be found a glandular or deeply staining body which corresponds to the "retortenförmigen Organe" of the German writers; and a long slender portion terminating in a point which constitutes the piercing stylet. The basal portions of the setae are contained within the head, but the long tapering stylets pass out through the buccal cavity, and eventually become lodged in a groove on the anterior face of the proboscis, which they traverse to its tip. The mandibular setae are free throughout their entire length, are somewhat stouter in build than the maxillary setae, and the cavity of the base of the seta is continued into the stylar portion in the form of a fine tube which traverses the stylet throughout its whole length. This tube, however, does not communicate with the exterior, but becomes closed when the stylet commences to taper off to form the pointed tip. In cross section, the mandibular stylet takes the form of an ellipse, one side of which, viz. the face which is applied to the maxillary seta of its side, is flattened (text-fig. 1).

The maxillary setae are rather more slender in form and, as they pass out from the head into the buccal cavity, each approaches the median line until, eventually, they become closely applied one to the other, so as to form a single piercing organ. At first this association consists merely of juxtaposition, but soon after the setae have left the buccal cavity they become more closely united. This is effected by the presence in each seta of a narrow groove on its inner face, which receives a corresponding ridge on the other seta so that the two parts become firmly fixed together. This interlocking becomes progressively more complete the nearer the tip of the organ is approached, but as far as can be determined, the two parts do not actually fuse together, though at the distal end it is apparently difficult to separate them. In the more proximal portions, however, the interconnection between the parts is not nearly so complete so that the outline of each component part can be clearly

made out in cross sections, and the two parts can be separated with comparative ease, and as this frequently happens during the process of section cutting, they are consequently often so seen in the sections. In addition to these interlocking grooves and ridges, two grooves are found traversing the whole length of each seta, with the result that, when the two setae are placed together, two channels are formed. These channels are unequal in size, and in the region of the buccal cavity the larger one is anterior to the smaller. Similar channels have been described by many authors as being present in other Hemiptera, and the larger channel is usually termed the suction canal,



Text-fig. 1. The upper figure is a section through the buccal cavity to show the interlocking arrangement of the maxillary sclerites and the grooves, in which the setae lie, formed between the maxillary sclerites and the epipharynx. (×363.)

The lower figure is a transverse section through the groove of the labium showing the setae *in situ*, and the interlocking of the maxillary stylets with the formation of the suction-canal and the efferent salivary canal. (×1466.)

(For explanation of lettering see p. 488.)

and the smaller one the efferent salivary canal. In the region where the maxillary setae are closely associated with each other, the resulting piercing organ is roughly rectangular in section (text-fig. 1), the long sides curving slightly inwards and the short sides outwards. The two component parts of the organ are, however, roughly triangular in outline, such as would result from the drawing of a diagonal across the rectangle. The middle portion of the section is occupied by the two canals, the suction canal being considerably larger than the efferent salivary canal. The interlocking ridges and grooves which hold the component parts together lie closely beside these canals along the line of the diagonal. The fine tubular continuation of the cavity within

the basal portion of the seta—such as has been described in the case of the mandibular setae—is, in the maxillary setae, either very much reduced or has become completely obliterated. Its presence could be detected in the buccal region, but beyond that it was not visible.

In many Hemiptera, both Homoptera and Heteroptera, the basal portions of both mandibular and maxillary setae are attached to the chitinous walls of the head by rods or plates of chitin which have been termed the mandibular and maxillary levers respectively. In *P. mali*, only the maxillary levers are present. These take the form of slender curved rods of chitin which pass from the inner face of the base of each maxillary seta, and, curving behind the seta, pass to and fuse with the outer lateral margins of the buccal folds (Pl. XXVIII, fig. 3). The mandibular setae are free throughout their entire length, and are devoid of any chitinous connection with the head capsule.

When the setae are examined from the lateral aspect in a cleared specimen of the insect, a remarkable feature with regard to them at once becomes obvious. This is the interesting course they describe after leaving the head and before they become lodged in the groove in the proboscis. Whilst still within the head, the bases of the setae—both mandibular and maxillary—lie well to either side of the median line, but, as the buccal region is reached, they gradually approach more and more towards the centre, until, as they pass into the buccal cavity proper, they occupy a median position. Whilst still anterior to the hypopharynx, both the mandibles and maxillary setae lie in grooves on the inner faces of the maxillary sclerites, but in the region of the hypopharynx the maxillary setae become more or less free and lie one on either side of that structure, and are separated by it. When the hypopharynx has been passed, the maxillary setae come together to form a single piercing organ but the mandibles remain separate. As has been indicated above, the setae in this region are lodged in channels formed between the epipharynx and maxillary sclerites. By this means the three piercing organs are kept in a definite relation to one another, the maxillary setae lying in the centre between the mandibles but separated from them by ridges of chitin which jut out from the inner faces of the maxillary sclerites. When the region of the maxillary sclerites has been passed, the setae are still held in position by being lodged in a groove on the inner face of the epipharynx, but now, instead of being separated from them, the mandibular setae lie in close juxtaposition one on either side of the approximated maxillary setae. The significance of these arrangements will be further considered when discussing the mechanism of suction.

So far, the setae have proceeded in practically a direct line, but, when they have traversed the buccal cavity, instead of passing directly into the groove in the labium, they curve sharply upwards, and enter the invagination of the ventral wall of the body between the pro-coxae which has been described above as the setal chamber. When the top of the setal chamber has been reached the setae, describing a complete semicircular curve, then pass into the groove

in the labium which they traverse to its tip. During their course from the buccal cavity to the tip of the labium, the setae become rotated about a central axis, so that, although the mandibles remain in the same relation to the maxillary setae, yet whilst at some points the three structures are parallel to the short axis of the body, at others they may be parallel to the long axis.

The Hypopharynx.

The hypopharynx is a short wedge-shaped structure which projects into the buccal cavity, and is formed by the fusion of the strongly chitinised posterior wall of the pharynx with the dorsal wall of the buccal cavity, in the same way as the epipharynx is formed by the fusion of the anterior wall or operculum of the pharynx with the labrum. The efferent salivary duct traverses the hypopharynx and opens out at its tip.

THE ENDOSKELETON OF THE HEAD.

The Tentorium (Pl. XXVIII, fig. 3).

The necessary support for the various structures and muscles connected with the mouth parts is provided by a chitinous framework situated within the head and composed of a system of apodemes or endosternites connected with the tentorium. The body of the tentorium consists of a hollow rod of chitin which traverses the head in a horizontal direction a little posterior and ventral to the cerebral ganglia, and over it the upper portion of the pharynx takes its backward curve as it passes into the oesophagus. This transverse bar (*tr. br.*) is held in position by two pairs of arms or supports which stretch between the ends of the bar and the cephalic skeleton. The anterior pair pass one from each end of the bar, almost vertically downwards towards the deflexed "front" of the head, with the chitin of which each becomes continuous at the point where the frons and clypeus join. The posterior pair extend between the ends of the transverse bar and the upper margins of the buccal folds. The transverse bar and both pairs of supports are hollow and their lumena intercommunicate so that the cavity within the transverse bar is in direct communication with the exterior through the lumena of the anterior supports, which open out on to the "front" of the head, and with the buccal cavity through the lumena of the posterior supports, which are continuous with the cavities of the buccal folds. In cross section, the transverse bar is circular in outline, but the shape of the supports varies, for in some places they are flattened, and longitudinal ridges or flanges are present to serve for the attachment of various muscles.

From this description it will be seen that the chitinous framework is comparatively simple and resembles the structures found in *Cicada* and allied forms, rather than the more complicated structures found in the *Aphidae*. Previous writers on the *Psyllidae* do not seem to have described it in detail. Witlaczil (1885) figures the transverse bar and gives some indication of the

supports, but is not very clear on the matter. Stough (1910) is rather vague, and makes no mention of the transverse bar beyond stating that the structure which Meek calls the tentorium is designated by Berlese as the transverse branch of the ipostoma, but figures structures which may correspond with the anterior and posterior supports. Crawford (1914) does not deal with the endoskeleton of the head, but in his figure of the mouth parts of *Psylla alni americana*, structures are indicated which from their position would correspond with the anterior and posterior supports.

The function of this framework is to serve as a suitable attachment for the various muscles connected with the setae and salivary pump.

The Salivary Pump (Pl. XXVIII, figs. 4–6).

The salivary pump of *P. mali* resembles in the details of its construction, similar organs which have been described in many Hemiptera. Seen from the anterior aspect, the pump consists of a hollow vase-shaped receptacle which is attached at its base to the wedge-shaped hypopharynx, and occupies a position in the head immediately behind the lower part of the pharynx. This pump chamber is closed above by a flexible chitinous membrane, to which is attached the pump muscle. If a transverse section of the head through the line of the pump is examined (Pl. XXVIII, fig. 4), it is seen that, in section, the chitinous membrane takes the form of a W, the outer arms of which are expanded and bent over and become continuous with the walls of the pump chamber. The pump muscle is attached to the upwardly directed centre of the W. The cavity of the pump chamber is in continuity with a fine channel—the efferent salivary duct—which traverses the hypopharynx, and which opens out on the tip of that structure. The pump chamber also receives, on its posterior face, the afferent salivary duct (Pl. XXVIII, fig. 5), a median structure formed by the junction of the ducts from the salivary glands, and which enters the chamber at a point a little below where the chitinous membrane becomes continuous with the posterior wall of the pump chamber. The whole apparatus is held firmly in position in the head by reason of the continuity of the chitin of its base with the hypopharynx, and the walls of the pump chamber are composed of thick chitin to ensure its stability.

The action of the pump is probably similar to that which has been described in other forms, the propulsive force being derived from the elasticity of the chitinous membrane. The necessary valvular arrangement in the case of the afferent duct is probably effected by the prolongation of the duct into the cavity of the pump chamber. The valve in connection with the efferent salivary duct is more difficult to imagine. Traversing the hypopharynx as it does, the walls of the duct are not collapsible, and no separate valve-like structure can be detected.

It is possible that a valve in connection with the efferent salivary duct may not be necessary, for the secretion contained in the afferent duct is always more or less under pressure, by reason of the activity of the salivary glands,

and it is possible that the slightest reduction of pressure within the pump chamber, would release any closing effect exercised upon the afferent duct, and the secretion would be poured into the chamber simultaneously with the raising of the chitinous membrane. This would preclude the possibility of extraneous fluid entering the chamber by the efferent duct.

The Pharynx.

The pharynx in *P. mali* presents no unusual features, and is constructed, as in so many Hemiptera, to perform a suctorial function. It varies in the shape of its cross section as it is traced from the point where it curves over the transverse bar, down towards the oral region. The posterior wall is more strongly chitinised than the anterior one, and in the upper portion is semicircular in outline, the thinner anterior wall forming the diameter of the semicircle. As the mouth is approached, the posterior wall assumes a more and more V-shaped form, and also becomes progressively more strongly chitinised. In this region the anterior wall also becomes V-shaped, but still remains thinner and lies inside the larger V of the posterior wall, so that the extremities of the arms of the two V's are joined together. The pharyngeal muscles are attached to the inner side of the base of this smaller V, and the suctorial effect is produced by a reduction of pressure within the pharynx, following upon the raising of this thinner wall or operculum by the contraction of these muscles.

THE MUSCULATURE OF THE HEAD.

In discussing the musculature of the head, it will be convenient to consider the muscles in groups in accordance with the portions of the head or appendages with which they are associated. The number of muscles concerned is large, considering the size of the parts, and to give separate names—many of which would have to be invented—to each, would be too cumbrous and lead to confusion. The system will therefore be adopted of indicating the various muscles in each group by numbers.

I. *The Antennal Muscles.*

The movements of each antenna are controlled by a set of five muscles which are attached around the base of the appendage where it articulates with the head capsule, and stretch from thence to the dorsal surface of the anterior support of the tentorium of its side. The muscles vary in size and consist of two large muscles, two small ones, and one very slender one.

II. *The Pharyngeal Muscles* (Pl. XXVI, figs. 2–4).

These muscles, by the operation of which the pumping action of the pharynx is effected, consist of a series of muscles arranged in pairs one above another, and are attached at one end to the centre of the lower portion of the operculum of the pharynx, and at the other to the inner side of the clypeus.

At their point of attachment to the operculum, the muscles assume a tendon-like character, but where they are attached to the clypeus they become much more expanded in outline.

III. *The Pump Muscle* (Pl. XXVI, fig. 2, Pl. XXVIII, figs. 5, 6).

This muscle is in reality a paired one, but where it is attached to the chitinous membrane of the salivary pump, the two parts are closely applied to one another and assume a tendon-like character. As the muscle is traced towards the dorsal surface of the head, it is found to divide into two halves, each of which runs into the angle formed by the junction of the posterior support of its side with the transverse bar of the tentorium. The muscle is consequently V or Y-shaped in outline, the upper extremities of the arms forming the points of attachment to the tentorium, and the base or stem representing the point at which the muscle is inserted into the chitinous membrane of the salivary pump.

IV. *The Supporting Muscles of the Tentorium.*

(*a*) Two muscles of moderate size stretch from the front of the head—vertex—to the ends of the transverse bar of the tentorium at the point where it joins on to the anterior supports. These two muscles lie immediately dorsal to the cerebral ganglia.

(*b*) Two muscles, much smaller in size than, but attached to the front of the head at the same point as (*a*), extend to the transverse bar and are attached to it one on either side of the median line, close to the centre. At the point where they join on to the front of the head, muscles (*a*) and (*b*) are closely applied, if not actually joined to one another.

(*c*) Two large double muscles, one on either side of the head, stretch from a point of attachment to the head formed by an invagination of the occipital sclerite, to the dorsal surface of the tentorium. They are joined to the latter at a short distance beyond the region where the posterior supports become continuous with the transverse bar.

(*d*) Two muscles, one on either side of the head, are attached at one end to the same point of attachment to the head as (*c*) but dorsal to them, and at the other end to the lower portion of the posterior supports of the transverse bar.

From their line of direction, the forces exerted by all these muscles, upon contraction, will be antagonistic to any downwardly directed traction exerted upon the chitinous framework. Since the framework is a fixed structure, it is clear that these muscles will not be concerned with moving any portion of it, but their function will be to counteract any displacing movement of the framework brought about by the pull exerted upon it by other muscles connected with the structures comprising the mouth parts, and thus serving to maintain the rigidity of the tentorium.

V. *The Musculature of the Setae* (Pl. XXVI, figs. 2–7).

(*a*) *The protractor muscles of the mandibles.* Each mandibular seta is provided with two protractor muscles, one of which is attached to the inner face of the base of the seta, and the other to the outer face. Suitable points of attachment to the seta for the muscles are provided by flange-like prolongations of the chitin of the base of the seta. At its lower end the inner muscle becomes continuous with the inner face of the maxillary sclerite and the outer muscle to its outer face. Of the two muscles, the inner one is shorter and less powerful than the outer. At their point of attachment to the mandible, the protractor muscles almost surround the base so that, in transverse sections, the seta appears to be embedded in muscle (Pl. XXVI, fig. 3).

(*b*) *The protractor muscles of the maxillary setae.* Like the mandibles, each maxillary seta is provided with two protractor muscles, but they lie close together and are attached to the outer face only of the base of the seta. Also the muscles are not so large as is the case with the mandibles. At their setal end, the muscles are attached to the outer side of the base of the seta, and special flange-like prolongations of the chitin do not appear to be present to serve as points of attachment. At their lower ends the muscles are joined on to the inner face of the maxillary sclerite.

With both mandibular and maxillary setae, the effect produced by the contraction of the protractor muscles will be to pull the bases of the setae towards the buccal region.

(*c*) *The retractor muscles of the mandibles.* These muscles, of which each mandible has two, are attached to the base of the seta at the opposite side of the inner face of the flange which serves as a point of attachment for the inner protractor muscle. The two muscles are large, lie closely together, and stretch upwards in the head towards the under side of the anterior support of the transverse bar, to the clypeal half of which they are attached. The muscles are relatively longer and more powerful than the protractor muscles.

(*d*) *The retractor muscles of the maxillary setae.* Each maxillary seta has two retractor muscles, but these are very closely applied to one another, so that in section they appear almost as a single muscle, but the dividing line between them remains clear. The muscles stretch from the inner face of the base of the seta to the under side of the anterior support of the transverse bar, but are attached nearer to the transverse bar than is the case with the retractor muscles of the mandibles.

When the retractor muscles of the mandibles and maxillary setae contract, they will tend to draw the bases of the setae further into the head.

VI. *The Muscles of the Head Capsule and Neck.*

In addition to the muscles already enumerated, there are a number of muscles attached to the various sclerites composing the head. They are arranged in groups, and are indicated briefly in the order in which they appear in a series of transverse sections of the insect.

(*a*) A group of five muscles runs from the occipital sclerite obliquely to the latero-ventral portion of the thorax.

(*b*) A group of three muscles runs from the occipital sclerite through the neck to the dorsal margin of the prothorax.

(*a*) and (*b*) serve to retract the head.

(*c*) A short stout muscle attached in front to the side of the neck, and behind to the ventral margin of the pronotum.

(*d*) A short stout muscle attached to the neck, in front, at about the same point of attachment as (*c*), but passing closer to the side of the body, and joins on to the dorsal surface of the side of the prothorax.

(*c*) and (*d*) control the movements of the head upon the neck.

VII. *The Muscles of the Oral Region.*

(*a*) A muscle attached to the gena anterior to the buccal cavity, traverses the head into the prothorax and joins on to the postero-lateral margin of the labial furrow.

(*a*) serves to further depress the head.

(*b*) A small muscle attached to the gena at the same point as (*a*) but passes obliquely upwards and is attached to the dorsal portion of the side of the body.

(*c*) A muscle attached to the dorsal surface of the buccal fold, traverses the head, and passes to, and becomes continuous with, the dorso-lateral margin of the labial furrow, close to the point of attachment of (*a*).

(*d*) A small muscle runs obliquely upwards between the outer lateral margins of the buccal fold and the dorso-lateral portion of the body.

(*e*) A small muscle runs from the lateral margin of the buccal fold almost horizontally forwards to the side of the body.

These muscles (*b*-*e*) regulate the movements of the sclerites surrounding the mouth.

VIII. *The Muscles of the Labium.*

(*a*) *The elevator muscles.* A long, slender muscle attached at its lower end to the first joint of the labium at a point where it originates on each side of the setal chamber, runs obliquely upwards and forwards and becomes continuous with the side of the body.

The contraction of this muscle elevates the proximal portion of the first joint of the labium, retracting it further into the labial furrow.

(*b*) *The muscles of the terminal joint.* In the expanded portion of the second joint of the labium, two pairs of muscles are present, one pair on each side of the groove, attached at their lower ends to the junction of the bulbular expansion on the anterior face of the second joint with the terminal joint, and stretching obliquely upwards, join on to the posterior wall of the labium at a much higher point.

From their position, these muscles can only control the movements of the

terminal joint, moving it forwards; or by the muscles of one side acting independently of those on the other, move the joint laterally to either side.

IX. *The Muscles of the Labial Furrow.*

Three sets of muscles are associated with the posterior portion of the labial furrow. Each arises from the dorso-lateral margin of the furrow, and

(*a*) runs upwards and forwards, and becomes attached to the middle of the side of the thorax,

(*b*) runs forwards but slightly downwards, becoming attached to the latero-ventral wall of the thorax, and

(*c*) runs almost vertically upwards and slightly forwards to the dorsal region of the body.

These muscles would counteract any displacing movement of the labial furrow, in whatever direction it should occur.

THE MECHANISM OF PIERCING.

In most of the papers which have been previously written dealing with the mouth parts of Hemiptera, it is rather curious that, although the structure of the parts concerned is often described in great detail, yet the actual means by which the piercing of the host is effected has been more or less overlooked or taken for granted. In many of these cases a complex system of apodemes comprising the endoskeleton, and protractor and retractor muscles associated with the piercing stylets have been described, and this, in most cases, has been considered sufficient. The protrusion of the setae has been attributed to the contraction of the protractor muscles, and the penetration of the host has been taken as a natural mechanical result of this protrusion. If the mechanism of piercing is examined more closely, however, it will be seen that this result does not always necessarily follow, and *P. mali* affords a good example of this. It has been described above, that the setae in *P. mali*, after leaving the head, do not follow a straight course into the proboscis, but describe a loop, which is contained within a special receptacle—the setal chamber—and then pass into the groove on the dorsal surface of the labium which they traverse to its tip. As a consequence of this, the direction of the distal portion of the setae, *i.e.* the portion contained within the proboscis when the latter is in its usual position, is at right angles to that of the bases of the setae. If the parts remain in this relation to one another during the act of piercing—and, as in its normal position the proboscis is nearly at right angles to the substratum, this is most probably the case—it is difficult to see how a force exerted along the line of the bases of the setae, which is the line of action of the force exerted by the contraction of the protractor muscles, can effect the protrusion of the tips of the setae with sufficient force to pierce the epidermis of the host. This could only happen if the setae were confined within a closely fitting tube throughout their whole length, which is not the case. If the mechanics of the problem

are considered, it will be seen that the only effect which would be produced by the contraction of the protractor muscles when the tips of the setae are resting against a resistant substratum, would be to increase the curve which the setae make when they pass from the head into the setal chamber. Even assuming that the proboscis was deflected during the act of piercing so that it lay more or less in the same line with the bases of the setae, this difficulty would still remain by reason of the loop of the setae which lies in the setal chamber.

The more the problem is studied, the more obvious it becomes that the considerations put forward above are not the only difficulties in the way of the conception that the protractor muscles are the sole means by which the setae are forced into the host plant. Many instances have been recorded in which the setae are thrust to varying, and sometimes considerable, distances into the host, in order to reach particular tissues from which the insect desires to obtain its food. If, keeping this fact in mind, the possible range of movement of the bases of the setae as effected by the contraction of the protractor muscles is considered, it will be seen that this range of movement is quite small compared with the distance to which the setae enter the host. An extreme case of this is met with in the case of *Chermes abietis* in which, according to Burdon (1908), the setae, which are considerably longer than the entire body, are almost completely inserted into the host plant. How could this possibly be brought about by the agency of the protractor muscles, whose range of action must be very much less than—in fact but a mere fraction of—the distance to which the setae penetrate? It may be argued that the act of piercing is not effected by a single contraction of the protractor muscles, but that with the first contraction, the setae are only forced into the tissues to a distance which is equal to the range of movement of the bases of the setae. This effected, the protractor muscles will relax and by a simultaneous contraction of the retractor muscles and a slight downward movement of the head, the bases of the setae will be restored to their original position. The protractor muscles would then again contract, and by a repetition of this cycle of movements, the setae would be driven in to the required depth. It will be shown later however, that for other reasons it is improbable that the force exerted by the contraction of the protractor muscles plays more than an insignificant part, if any at all, in the actual operation of piercing.

Whilst considering the difficulty arising from the limited range of action of the protractor muscles, it will be well to indicate another difficulty of the same kind. It has been shown by a number of authors that in many cases in the Hemiptera, both Heteroptera and Homoptera, the bases of both mandibular and maxillary setae are directly attached to the head capsule by rods or plates of chitin, which have been termed the mandibular and maxillary levers. These attachments will further limit the range of movement of which the bases of the setae are capable.

A further point of difficulty is that the portion of the setae which lies in

the proboscis is not completely enclosed by it, but the setae lie in a groove, which is open anteriorly, in the anterior face of the labium. The extent to which the setae are enclosed varies in different species and also in different parts of the proboscis, but in general, the setae are more firmly held at the tip of the labium than in the more proximal portions. It is usually suggested that the groove serves to support the setae whilst they are being driven into the host, and to prevent bending; but again, if the mechanics of the problem are considered, the matter is not so simple. The setae are extremely fine, delicate, and flexible structures, and when their tips are resting against a resistant surface, the effect of exerting a force upon them such as would be derived from the contraction of the protractor muscles, would be to cause them to bend; and although at the tip of the proboscis the groove is sufficiently contracted to enclose them in a moderately firm grip, yet in other parts of the labium where the groove is not so strongly developed, the bending of the setae could not be controlled, and they would protrude through the open portion of the groove, with the result that a great part of the driving force would be wasted. This difficulty must be materially greater in those cases such as the *Chermidae* and *Psyllidae*, etc. where the setae are much longer than the proboscis.

Awati (1914) states that in *Lygus pabulinus* the labium is bent during the act of piercing in order to enable the setae to penetrate further into the host. His description of the process is as follows (p. 728):

"(1) *The stylets inside a leaf.*

The insect begins to feel the surface of a leaf with the sensory hairs at the tip of the proboscis. It is trying to find a good place for piercing. When it is found, the proboscis is applied to it, the stylets are driven forward, the protractors contract, and the epidermal layer is pierced, however thick it may be.

(2) *The bending of the proboscis.*

Once in, the stylets are pushed down into the tissue by direct mechanical force, *i.e.* by the bending of the proboscis. This feature has already been alluded to. It increases artificially the protrusion of the stylets and enables them to reach the tissues which contain food...."

In describing the labium, Awati says (p. 696): "The labrum and the labium together keep the stylets in place. In the first segment, where the labial groove is too flat and shallow to do it, and where the labium has a bend inwards, thereby leaving the stylets free, the labrum encloses them in its groove. Distally the labium takes over this function of holding the stylets, since its groove becomes deeper and deeper. Thus the stylets are always found in the groove of one or the other, and are prevented from that lateral movement which would make piercing and sucking impossible.

The labium protects the stylets in the groove, but its more important function is very ingenious. The stylets are very thin, needle-like structures

which have, however, to pierce the tough and cuticularised epidermis of a leaf. As they are very delicate, they would bend in the act of piercing, were they not enclosed in the proboscis. The lumen of the tubular tip of the proboscis is so small that the stylets fit into it tightly (text-fig. 8). There is no empty space in it for them to bend. The tip of the labium is closely applied to the surface of the leaf; the protractor muscles of the stylets contract; and the stylets are forced out of the proboscis and driven against the epidermis, which they cannot fail to pierce. Once in, their forward progress to the required tissue is mechanical owing to the bend of the labium at the first joint.

It is thus obvious that the labium is an important structure in the sucking apparatus of this insect; it is one, moreover, on the structure of which stress has not been laid by previous writers."

These statements seem to contain some contradiction and confusion of ideas, which is unfortunate in what is evidently a serious attempt to explain the operation of piercing. The author emphasises the fact that the stylets are very delicate and would bend if they were not enclosed within the groove in the proboscis and yet goes on to say that once the setae are in (the tissues of the plant) their further progress is mechanical owing to the bending of the labium. The latter statement is clearly a contradiction of the first, for the author does not seem to have realised that if the labium bends the setae must leave the groove if the advantage which he claims, viz. the further protrusion of the stylets, is to accrue: for if they still remain within the groove no increased protrusion would result. If therefore the setae do leave the groove, and remain in the same straight line with that portion of them which has already entered the host, it is clear that they will lose that support of the groove throughout a great part of their length which according to the author is essential for the successful piercing of the host, and when a further driving force is applied to them they would bend. The author passes over this serious difficulty by stating that once the setae have entered the host, their forward progress is mechanical, owing to the bend of the labium. This is unfortunately too vague, and leaves a great deal to the imagination of the reader. For what is the force which causes this forward "mechanical" progress? There appear to be only two alternatives; either the force produced by the further contraction of the protractor muscles, or some pressure exerted by the lowering of the position of the head and body in relation to the substratum. Either of these would exert a driving force along the length of the setae but, as has been pointed out above, the major part of this would be vitiated by the bending of that portion of the stylets which was not contained in the groove of the proboscis, and although a slight penetration of the tips of the setae might occur, this would be quite inadequate to the result desired.

This bending of the labium occurs also in other piercing insects outside the Hemiptera, as is admirably shown by Nuttall and Shipley (1901) in their figure of a female *Anopheles maculipennis* feeding. Here the trophi are free from the labium for the greater part of their length and the latter is bent into

the form of a backwardly directed loop. The authors suggest that the trophi enter the skin by means of the same elastic force which induces the sharpened end of a piece of whalebone to pierce a soft body if the other end is pushed towards the surface. This is criticised later by Cragg (1913) who, after a careful discussion of the subject, arrives at the conclusion that piercing is effected in stages, and that the extremely rapid protraction and retraction of the maxillae lacerates the tissues and paves the way for the entry of the other mouth appendages. This, however, does not help very much in the elucidation of the problem of piercing in the Hemiptera.

As a final addition to the difficulties of the problem enumerated above, it may be mentioned that the writer (Grove, 1909) in describing the anatomy of *Siphonophora rosarum* stated that in that insect only the maxillary setae were provided with protractor muscles. This led the writer to suggest a method for the protrusion of the setae, which in the light of fuller knowledge requires considerable modification, but the interest of the absence of the mandibular protractor muscles remains.

From all these considerations therefore, it would appear that the penetration of the host is not effected in many Hemiptera, and certainly not in the case of *P. mali* in the way which has hitherto been accepted, namely by means of a driving force exerted along the length of the stylets as a result of the contraction of the protractor muscles. The question now remains to arrive at some other interpretation of the mechanism and method of action of the parts involved, which will fit in more closely with the mechanical laws concerned.

The problem which has to be solved, resolves itself into the mechanical means necessary to force a long, extremely slender, flexible, pointed body to some depth into a moderately hard substance. It may be illustrated by considering how a piece of fine, flexible steel wire can be driven most readily into a piece of moderately hard indiarubber. It is obvious at the outset that the result will not be attained by applying one end of the wire to the surface of the rubber, and exerting pressure at the opposite end. This will merely cause the wire to bend, and very little penetration will be effected. Since it is the bending of the wire which interferes with the attainment of the desired result, the obvious remedy is to introduce some mechanical device which will overcome this. This might be effected in two ways; either by enclosing the wire within a closely fitting rigid tube so that bending would be impossible, or by applying the driving force to such a small portion at a time that the possibility of bending would be practically eliminated. This latter method would, in practice, be effected by the use of a pair of strong forceps or pincers; the wire would be firmly gripped at a short distance from the pointed end, and the projecting portion forced into the rubber. This accomplished, the grip of the forceps would be released, moved a little further up the wire, the grip applied once more, and a further portion forced in. This series of operations would then be repeated until the wire had been driven in to the required depth.

Returning now to the consideration of the mechanism present in the insect, is it possible to apply either—or both—of these methods? From what has been recorded above, it is clear that the first method can be ruled out at once, at any rate as far as *P. mali* is concerned. In this insect the setae are free after they leave the epipharynx until they are lodged within the setal chamber, and although, within the proboscis the bending of the setae would be controlled to some extent by the groove in which they lie, yet in the proximal region of the labium they could still bend in one direction, namely through the open side of the groove. There is therefore no structure present which would serve as a closely fitting tube to restrain the bending of the setae.

At first sight, the alternative mechanical device suggested scarcely seems to offer a solution, for it is not at all obvious what structure in the mechanism of the mouth parts could possibly take the place of the gripping instrument—forceps or pincers—used in the illustration.

The only portion of the mouth parts which, from its position with relation to the setae, could possibly function in this way, is the labium or proboscis. In the description of the labium of *P. mali* it was stated that as the tip of the organ is reached, the character of the groove changes somewhat. In this region, the walls of the groove and of the labium itself, are more strongly chitinised, and the lumen of the groove becomes smaller so that the setae are more closely enclosed by it. In fact, at the tip of the proboscis, the relation of the groove to the setae is such, that a very little compressing force would be necessary to ensure the latter being held in a firm grip.

It is evident therefore that the tip of the labium will provide the instrument for gripping the setae, but the next problem to solve is the origin and nature of the driving force which is to act through the labium to thrust the setae into the plant. There appear to be two possibilities. The first is, that the force might result from downward pressure exerted by the closer approximation of the body of the insect to the substratum, the labium being held rigid the while. The objections to this are that it is cumbrous, and that the labium is not particularly rigid throughout its whole length, the first segment particularly being composed of relatively thin chitin. The other possibility is that the force arises as a result of increased pressure of the body fluid contained within the labium. This increased internal pressure would cause the organ to become turgid and elongated, since the flexible portions between the segments of the proboscis, and also part of the flexed first segment, would become straightened out. Consequently, provided the body of the insect was held rigid, the tip of the labium would be pushed down towards the substratum. Another consequence of this increased internal pressure would be that the grip of the tip of the labium would be increased, for the pressure would tend to bring the margins of the groove closer together, thus further reducing the space enclosed. In this way, the two desiderata, the grip on the setae, and the downward driving force, would arise simultaneously. On this hypothesis, the sequence of events during the operation of piercing would be as follows:

The insect having, by means of the tactile hairs at the tip of the proboscis, selected the spot at which it desires to pierce the plant, the labium would be drawn up for a short distance by means of the elevator muscle, exposing a small portion of the pointed ends of the stylets which would protrude from the tip. The internal pressure of the body fluid within the labium would then be increased by the forcing of more fluid into it from the body, with the result that the tip of the labium would grip the setae, and, with the consequent elongation of the organ, the projecting portions of the setae would be driven into the plant. This operation completed, so that the tip of the labium would be in contact with the substratum, the internal pressure would be slackened, and as a result of this slackening two things would happen. First, the grip on the setae would be relaxed, and second, the decreasing turgescence of the organ would result in its becoming shorter so that the tip of the labium would have travelled a short distance upwards along the setae. The elevator muscle would also assist in this. The tip of the labium would now be in the right position again to take a grip of the setae in order to force in a further portion. An increase in the internal pressure of the body fluid within the labium again occurring, the grip on the setae would be re-established, and the resulting elongation of the organ would force the projecting portion of the setae into the host. By the continued repetition of these processes, the setae could be driven into the host to any desired length, limited only by the length of the stylets.

On this hypothesis, it can be readily understood, how in those cases where the setae are much longer than the proboscis, they can be forced into the plant, and the portion not contained within the labium, and which under ordinary circumstances remains in the form of a loop outside the proboscis (*e.g. Chermes*) or is lodged in a special setal chamber (*e.g. Psylla*), is brought into use. But although the hypothesis gives a feasible explanation of some of the hitherto almost inexplicable cases, it also presents some difficulties. The first to occur to the mind of the critic is that it does not take into account the elaborate mechanism of protractor muscles contained within the head, to which, previously, the function of performing the operation of piercing has been attributed; and it may be argued that it is scarcely likely that these structures would be so developed unless they had a definite function to perform. It has been suggested by many writers that, when the setae have been forced into the plant, they do not remain in a state of rest in the wound which they have made, but are kept in constant motion in order to lacerate the tissues, and so maintain a supply of fluid. In the hitherto accepted view, this was effected by alternate slight contractions and relaxations of the protractor and retractor muscles, resulting in slight protrusions and retractions of the setae. On the hypothesis which has just been elaborated, this would represent practically the entire function of these protractor and retractor muscles. The suggestion is, that when the setae have penetrated to the required depth, with the result that they now have completely straightened out from base to tip, the forces exerted by the contractions of these muscles can now operate

successfully and by moving the setae up and down in the wound to the extent of their limited range of movement, cause a continued laceration of the cells in their vicinity. It is possible too, that the mandibular setae move independently of the joined maxillary setae.

This suggestion of the true function of the protractor and retractor muscles is supported by the case of certain stages in the life-history of *Chermes*. Burdon (1905) in describing these stages, says that once the insect has established itself in a suitable position, she never quits the spot, but remains there until her death, so that during her lifetime she probably only performs the complete operation of thrusting in the very long setae once. As far as is known to the writer, the anatomy of the mouth parts of this species has not been described, but there is no reason to suppose that were this done, the same complicated system of protractor and retractor muscles would not be found, such as has been described in many allied *Aphidae*. Consequently, from the peculiar habits of *Chermes*, these muscles would be used almost entirely in the way that has been suggested as their true function, namely, in maintaining the supply of sap by the continued laceration of the tissues.

Another possible criticism which may be put forward if the hypothesis is to be applied in general to piercing insects, and in particular to other Hemiptera, is that in some cases the labium is bent whilst the later stages of penetration are being effected. This is more particularly so in those cases where the setae are not longer than the proboscis, and the bending of the labium is a device, as suggested by Awati (1914), by which more deeply seated tissues are reached. But as a question of mechanics, the protractor force of the labium would be increased and not diminished by this flexion, for in this condition the tendency of the increase of pressure of the body fluid within the labium would be to cause the organ to straighten out, and thus would serve as an additional protractor force to that produced by the normal elongation of the organ following upon its increased turgescence.

A further objection which may be urged is that the force which would be exerted in the way that has been suggested, would not be sufficient to produce the desired result. But in support of the hypothesis, examples might be quoted of the use of the internal pressure of the body fluid to effect an even more difficult result. A good example, which is distinctly *à propos* to the case, since the structure concerned is in connection with the head, is the *ptilinum* which is present in so many of the freshly emerging imagines of the *Muscidae* and other Diptera. As is well known, this structure consists of a sac formed by the eversion of the integument of the front of the head, and by the expansions and contractions of this sac, produced by variations in the internal pressure of the body fluid contained within it, the newly emerged insect, although it is in a delicate condition owing to the fact that its chitinous exoskeleton has not yet completely hardened, is able to force a passage large enough for its whole body through, in some cases, a thick layer of moderately hard earth in which the pupa, from which it emerged, was buried.

From this example it is clear that a very considerable force can be exerted through a suitable organ by the variations in the internal pressure of the body fluid contained within it, and quite commensurate with, if not greater than, the force which would be derived from the contractions of the protractor muscles to which hitherto the whole of the act of penetration has been attributed.

The progress of the discussion may now be conveniently summarised. It has been shown that in the case of *P. mali* the penetration of the setae into the host cannot be effected by the agency of the protractor muscles, and the difficulties in the way of the application of the conception (that the action of the protractor muscles alone can produce the result which has been ascribed to them) to other cases, have been enumerated. As an alternative it is suggested that in *P. mali* the forcing of the setae into the host is brought about through the agency of the labium, actuated by variations in the internal pressure of the body fluid contained within it. It is further suggested that this hypothesis may explain such cases as *Chermes* where the setae are very long and not wholly contained within the proboscis. Various possible objections to the suggestion have been indicated, and answers to them given.

The next problem to consider is how the setae are withdrawn from the host, when the insect wishes to move to another spot. From what has gone before, it is evident that, just as the range of movement of the protractor muscles is insufficient to account for the depth to which the setae penetrate, so equally, the range of movement of the retractor muscles is insufficient to withdraw the stylets, though it is certain that by their participation in the to-and-fro movements of the setae, they will loosen them in the wound preparatory to withdrawal. There remain two alternatives; either the setae are dragged out of the wound by the raising of the whole body; or that the labium is again instrumental in this operation. To the first suggestion there are some objections. Although the maxillary setae are connected with the endoskeleton of the head by means of the maxillary levers, the mandibles in *P. mali* are quite free, so that any traction exerted by the raising of the head or body would only be operative to any great extent upon the maxillary stylets, and the mandibles would be left behind, unless the retractive force of the retractor muscles of the mandibles was sufficient to retain them in their proper relation to the maxillary setae. It is scarcely probable, therefore, that this suggestion is a true explanation of what occurs in *P. mali*, though in other cases, where both mandibular and maxillary levers are present, it may be operative to a limited extent. Also in those piercing insects where the articulation of the head to the body is not strong, and the neck is composed of thin conjunctival membrane, the withdrawal of the setae could not be effected in this way. Considering the alternative suggestion, viz. the instrumentality of the labium, it is difficult to see how the force exerted by the variations in the pressure of the body fluid contained within the organ, as suggested for the driving in of the setae, could, alone, operate in their retraction. This is because the driving

force is only applied when the labium becomes turgid and is consequently protruded. In its retracted state, the labium is comparatively flaccid and its hold upon the setae is lessened. As has been stated above, the major part of the first segment of the labium is fused to the under side of the body, and the free portion of the labium lies almost hidden between the articulation of the first pair of legs. If therefore the thorax is raised, the labium will be raised with it and if at the same time the labium is in a state of turgescence and consequently has a firm grip of the setae, a powerful retractile force will be brought to bear upon the setae and will withdraw them bodily from the wound. In the preliminary stages, some assistance is doubtless afforded by the elevator muscles of the labium though it is scarcely probable that these can do more than help to prevent the labium from being torn out of the body.

THE MECHANISM OF SUCTION.

The problem of the means whereby the juices obtained from the host are conveyed into the alimentary canal in the Hemiptera, is one which has received more attention from previous writers than the operation of piercing, but there are some points in connection with it which have either been taken more or less for granted or require further elucidation. By way of illustration the process of suction as described in two recent papers may be given.

Awati (1914) in describing the mechanism of suction in *Lygus pabulinus*, the Potato Capsid Bug, sums up the factors concerned (p. 731) as:

"(i) Capillarity in the suction canal, helped by the turgidity of the cells.

(ii) Suction produced by the vacuum through the raising of the operculum.

(iii) The peristalsis in the oesophagus by means of the constrictors.

(iv) The valvular action, which prevents the sap from flowing back into the oesophagus from the stomach."

He further adds: "The pharyngeal duct hangs into the suction canal and is immersed in the sap. A question arises whether it is possible for the sap to avoid the duct and flow into the body cavity from the suction canal. The sap cannot do so because (i) there is no difference of pressure to force the sap into the body-cavity, and because (ii) there is active suction through the pharyngeal duct."

"Another important thing for suction is that the suction- and ejection-canals must be separate and distinct from each other. The least intercommunication will stop the whole mechanism. Also one canal cannot serve two contradictory purposes—one of sucking and the other of ejecting saliva. The whole mechanism, therefore, depends upon the presence of the two canals."

The author also says (p. 729): "Before the sap is sucked through the suction canal, it seems that saliva is injected into the wound made by the stylets."

Davidson (1914) describing the same process in *Schizoneura lanigera*, says (p. 326):

"When the stylets have been forced into the desired part of the plant-tissues, suction commences.

Owing to the very minute lumen composing the suction-canal, it is very probable that the plant juices ascend up this canal, largely by means of capillarity, and there is the further factor of the pressure of the sap itself.

As the divaricator muscles of the pharynx contract, they pull out the flexible dorsal wall of the pharynx, thus greatly enlarging the lumen of that structure. This causes a sucking action, and as the plant-juices make their way from the suction-canal up the pharyngeal duct, they are drawn from the latter into the pharynx proper."

It is clear that in considering the question of the mechanism of suction, two problems present themselves. First, the flow of the sap from the host along the suction canal, and, second, the ejection of the saliva down the salivary canal. In connection with the first, it is seen that Awati and Davidson both suggest that capillarity and the pressure of the sap are important factors, and this would certainly appear to be the case. The extent to which capillarity assists in the process is difficult to determine, since there are so many factors, some of which would vary under different circumstances, about which accurate information is not easily obtainable. It is known that the height to which a liquid will ascend a fine tube by the action of capillarity is dependent upon the surface tension and the density of the liquid, the diameter of the tube, and the angle which the liquid makes with the tube. Of these, only the diameter of the tube can be readily determined. The others: surface tension, density, and angle of junction with the tube would vary according to the composition of the sap. Since, however, the rise of the liquid in the tube is inversely proportional to the diameter of the tube, it is clear that in the case of a tube of such a fine bore as that of the suction-canal, the distance to which the liquid will rise will be appreciable, unless the liquid is very viscous. The part played by the pressure of the sap will also be a variable quantity, depending upon the kind of tissue to which the setae penetrate. If they enter the sap-bearing xylem, the pressure of the sap might be a definite factor, but if they merely puncture the cortical cells, and lacerate them, it is not at all easy to see how the osmotic pressure of the cells could be of any assistance, for once the cells were torn, the cell-sap would pour out, but the osmotic pressure would disappear. In neither of the descriptions quoted above, is the suctorial effect produced by the pharynx suggested as assisting in the conveying of the sap along the suction-canal, but it is possible that it may do so. The chief difficulties in the way are that there is no physical continuity between the pharynx and the suction-canal, and that the suction-canal itself is —at least in *P. mali*—not a complete tube throughout its whole length. Under these circumstances, it would seem that any suctorial effect produced by the pharynx would not be transmitted to the fluid in the suction-canal, but would merely draw in such fluid, or air, that surrounded the orifice of the pharynx at the time. But if the conditions which obtain during the process of suction

are considered, it will be seen that these difficulties are, perhaps, not so great as to be insurmountable. In describing the maxillary setae of *P. mali*, it was shown that the maxillary setae as they leave the head, pass out one on either side of the hypopharynx, and then are immediately received into a groove or channel formed by the apposition of ridges on the inner faces of the epipharynx and maxillary sclerites, which in this region are so constructed that they interlock, and, consequently, are firmly held together. The stability of these sclerites would also be assisted by the oral muscles VII (*b*—*e*), the action of which would be to press the sclerites together against the roof of the buccal cavity. The effect of the enclosing of the setae in this channel in this way, would be that the termination of the pharynx and the proximal end of the suction-canal would be maintained in intimate relations with one another. Presuming then that the sap from the host rises up the suction-canal immediately the setae are inserted into the plant by the action of capillarity, assisted by whatever help may be derived from the pressure of the sap, it will follow that the proximal end of the canal and the orifice of the pharynx will be bathed in the fluid. As a consequence of this, any interstices in that portion of the canal where the interlocking of the setae is not so perfect will be filled up, and there will be direct "physical" continuity between any liquid within the pharynx and that contained in the suction-canal. If now a reduction of pressure, or tension, is produced inside the pharynx by the raising of the operculum by the pharyngeal muscles, a pull will be exerted upon the column of fluid in the suction-canal in a way similar to that which it has been suggested is exercised by the osmotic pressure in the leaves of a plant upon a contiguous column of sap. This, combined with the peristaltic action of the pharyngeal muscles, will ensure a continuous flow of fluid along the suction-canal and pharynx into the oesophagus. This then is the way in which it is suggested that the transference of the sap from the host-plant to the insect takes place.

The second problem, that of the injection of the salivary secretion into the host, also presents some points of difficulty. The chief of these is again, the lack of physical continuity between the termination of the efferent salivary duct and the efferent salivary canal which traverses the maxillary setae. It is not easy to see, therefore, why the salivary secretion when it is ejected from the efferent salivary duct by the action of the salivary pump, should pass down the salivary canal and enter the wound. It appears just as probable that it would be poured into the buccal cavity, or even into the suction-canal. Another point to be considered is that if the suggestion made in considering the process of suction is true, that the sap rises in the suction-canal by means of capillarity, it will apply equally to the salivary canal, so that the propulsive force exerted by the salivary pump will not only have to eject the secretion, but also overcome the resistance of the capillary attraction. This makes it imperative that there should be as little leakage of force as possible, and that the connection between the two channels should be as close as possible. As

has been indicated in the case of the connection between the pharynx and the suction-canal, the maintenance of the parts in the correct relation to one another to effect this continuity is brought about by the enclosing of the maxillary setae within the channel formed between the epipharynx and the maxillary sclerites, which results in their being held firmly in juxtaposition with the end of the hypopharynx; and as the orifice of the pharynx is immediately dorsal to the hypopharynx and that of the efferent salivary duct is at its tip, it follows that the former will be directly opposite to the suction-canal and the latter to the efferent salivary canal. Also, since the maxillary setae pass out of the head one on either side of the hypopharynx, and the whole apparatus is maintained in a condition of stability by the action of the oral muscles, the hydrostatic continuity of the two salivary channels will be established, and fluid ejected from the salivary pump through the efferent salivary duct will pass uninterruptedly down the efferent salivary canal. The presence of fluid around the junction of the two channels will, by its sealing action, also assist in effecting this continuity.

CONCLUSION.

The method by which the operations of piercing and sucking are performed in the Hemiptera is a subject of great interest, and the conditions which have been revealed by the study of the head and mouth parts in *Psylla mali*, are such that the working of these parts during these operations is not understandable by the hitherto accepted explanations. A method by which these results are attained in this insect has therefore been suggested, which, although referring strictly to *P. mali*, presents possibilities which may be capable of a wider application, and opens up a field of research, along similar lines, into the conditions which obtain in other forms, especially the more specialised ones, such as the Chermidae and Coccidae, which should be fruitful of results. Unfortunately, in *P. mali*, the way in which the labium is buried between, and hidden by, the procoxae, precludes confirmation of the suggestions by direct observation, but, possibly, investigations with other forms may throw further light upon the subject.

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EXPLANATION OF PLATES XXVI—XXVIII.

PLATE XXVI.

Fig. 1. A transverse section through the head passing through the anterior supports of the transverse bar. (×75.)

Fig. 2. A transverse section through the head showing the retractor muscles of the setae. (×234.)

Fig. 3. A transverse section through the head showing the protractor muscles of the setae. (×234.)

Fig. 4. A transverse section through the head showing the commencement of the maxillary sclerites. (×234.)

Fig. 5. A transverse section through the buccal cavity. (×140.)

Fig. 6. The musculature of the mandible. (×234.)

Fig. 7. The musculature of the maxillary seta. (×234.)

PLATE XXVII.

The figures in this plate are taken from a series of serial sections through the insect to show the arrangement of the sclerites in the buccal cavity, and the origin of the setal chamber and the labium.

Fig. 1. A transverse section through the buccal cavity two sections posterior to the hypopharynx. (×217.)

Fig. 2. Three sections further back from 1. (×217.)

Fig. 3. The next section but one. The setal chamber is now beginning to appear. (×217.)

Fig. 4. Six sections further back from 3. The epipharynx has now almost disappeared, and the setal chamber is very marked. (×217.)

Fig. 5. The fourth section from the last. The commencement of the first joint of the labium has now appeared. (×217.)

Fig. 6. The sixth section from 5. The setal chamber and the first joint of the labium are now quite clear. (×217.)

Fig. 7. Two sections further back from 6. The distal portion of the labium has now come into the section, and is nearing the proximal portion which is becoming separated from the body. (×217.)

Fig. 8. Three sections posterior to the last. The junction of the proximal and distal portions of the labium is now complete, and the organ is nearly separate from the body. (×217.)

Fig. 9. The next section but one. The labium is now free, and projects downwards between the procoxae. (×217.)

PLATE XXVIII.

Fig. 1. A semi-diagrammatic figure of the head region to show the depression of the head and the position of the labium. The upper genal cone and procoxa are not shown in order that the front of the head and the labium, which would be otherwise hidden, may be seen. (×53.)

Fig. 2. The details of the buccal region and the labium. (×106.)

Fig. 3. The chitinous framework and tentorium seen from the posterior aspect. (×234.)

Fig. 4. The details of the salivary pump. (×893.)

Fig. 5. A side view of the salivary pump, showing the position of entry of the afferent salivary duct. (×420.)

Fig. 6. A section through the salivary pump showing the attachment of the pump muscle. (×420.)

REFERENCE LETTERING.

aff. sal. du. Afferent salivary duct.
ant. Antenna.
ant. mus. I Antenna muscle I.
ant. supp. Anterior support of the transverse bar of the tentorium.
buc. cav. Buccal cavity.
buc. fld. Buccal fold.
ceph. mus. VIa. Cephalic muscle VIa.
chit. memb. Chitinous membrane of the salivary pump.
clyp. Clypeus.
div. sal. gl. Diverticulum of the salivary gland.
eff. sal. du. Efferent salivary duct.
el. mus. VIIIa. Elevator muscle VIIIa of the labium.
epiph. Epipharynx.
eye. Eye.
ge. con. Genal cone.
grv. labi. Groove in the labium.
hypoph. Hypopharynx.
1st leg. First leg.
labi. Labium.
labi. fur. Labial furrow.
labr. Labrum.
max. Maxillary seta.
max. lev. Maxillary lever.
max. scl. Maxillary sclerite.
mnd. Mandible.
mus. IXc. Muscle IXc of the labial furrow.
n.s. Central nervous system.
oc. Ocellus.
oes. Oesophagus.
or. mus. VIIa,b,c,d. Oral muscle VIIa, b, c, d.
ph. Pharynx.
ph. mus. II. Pharyngeal muscle II.
post. supp. Posterior support of the transverse bar of the tentorium.
protr. max. Vb. Protractor muscle Vb of the maxillary seta.
protr. mnd. Va. Protractor muscle Va of the mandible.
pu. ch. Chamber of the salivary pump.
pu. mus. III. Muscle III of the salivary pump.
reto. org. "Retortenförmige Organe."
retr. max. Vd Retractor muscle Vd of the maxillary seta.
retr. mnd. Vc. Retractor muscle Vc of the mandible.
sal. du. Duct from the salivary gland.
sal. can. Efferent salivary canal.
sal. pu. Salivary pump.
se. Setae.
se. ba. Bases of the setae.
se. ch. Setal chamber.
suc. can. Suction-canal.
tent. mus. IVb,c,d. Supporting muscles IVb, c, d of the tentorium.
tr. br. Transverse bar of the tentorium.

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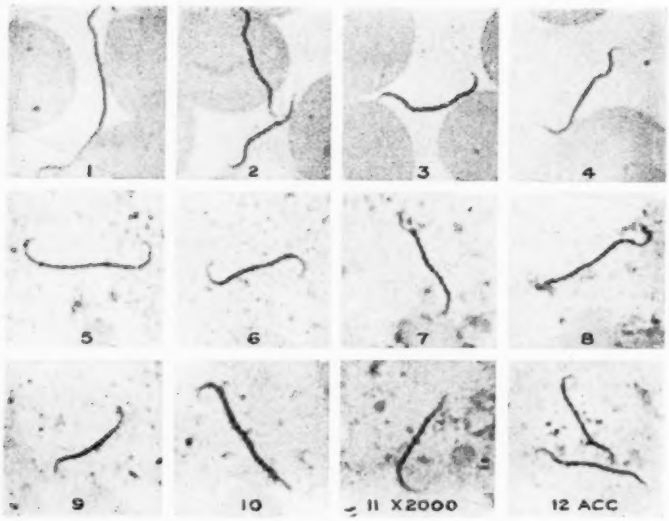

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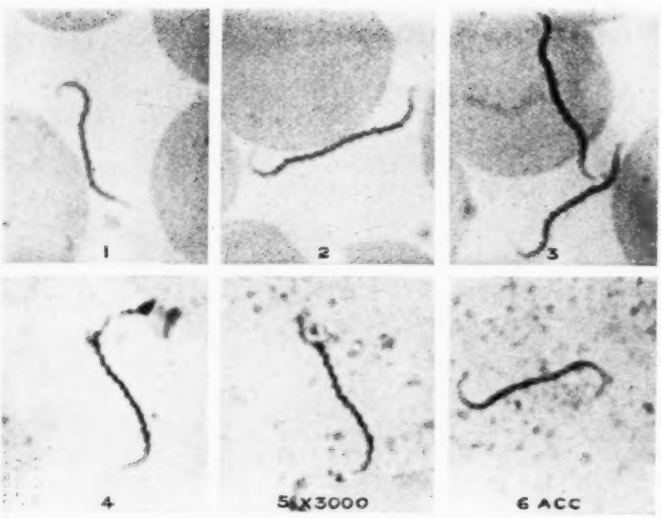

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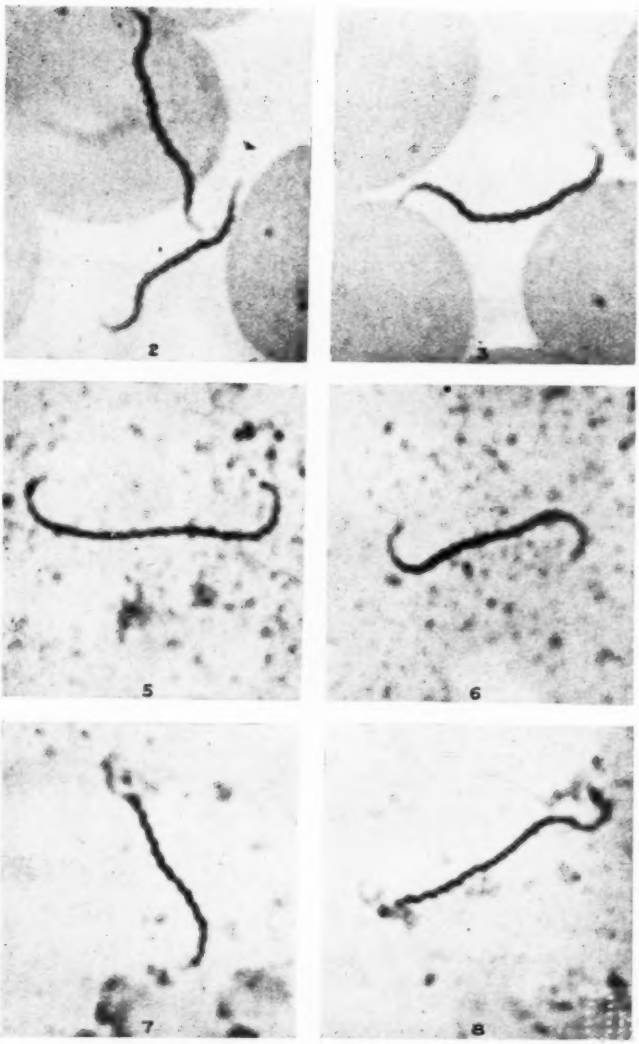

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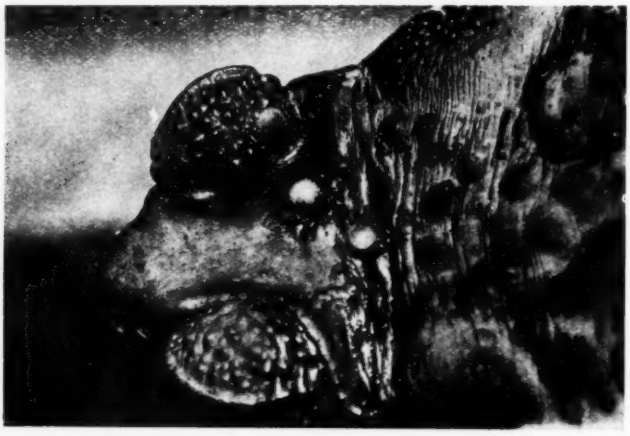

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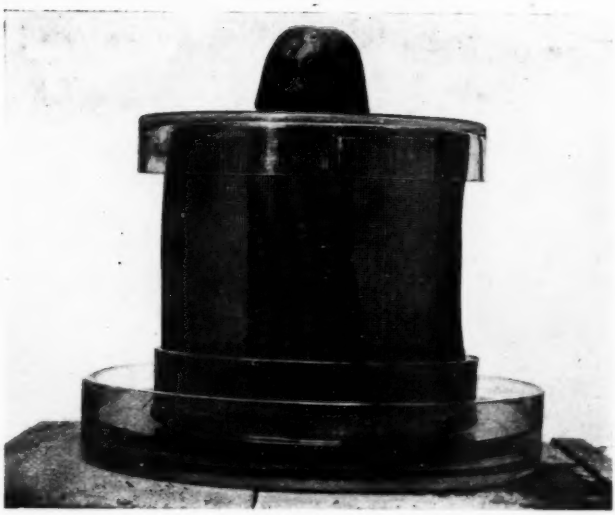

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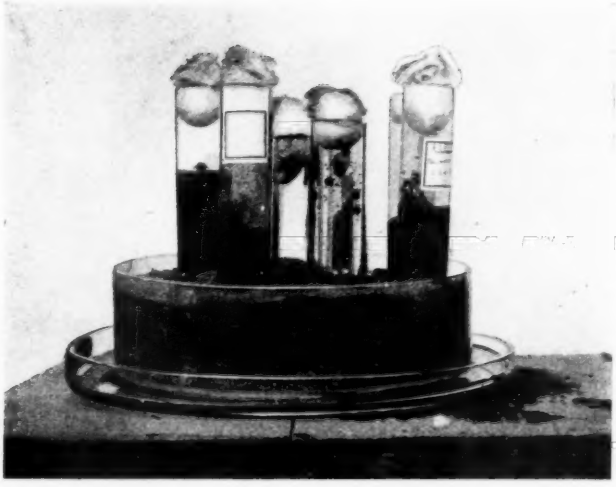

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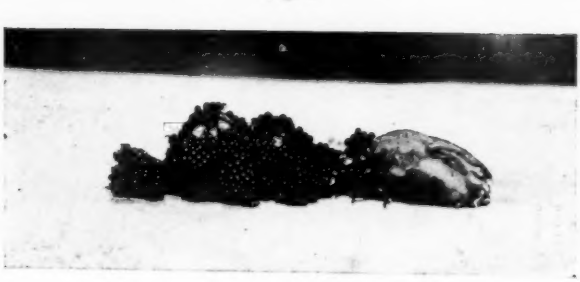

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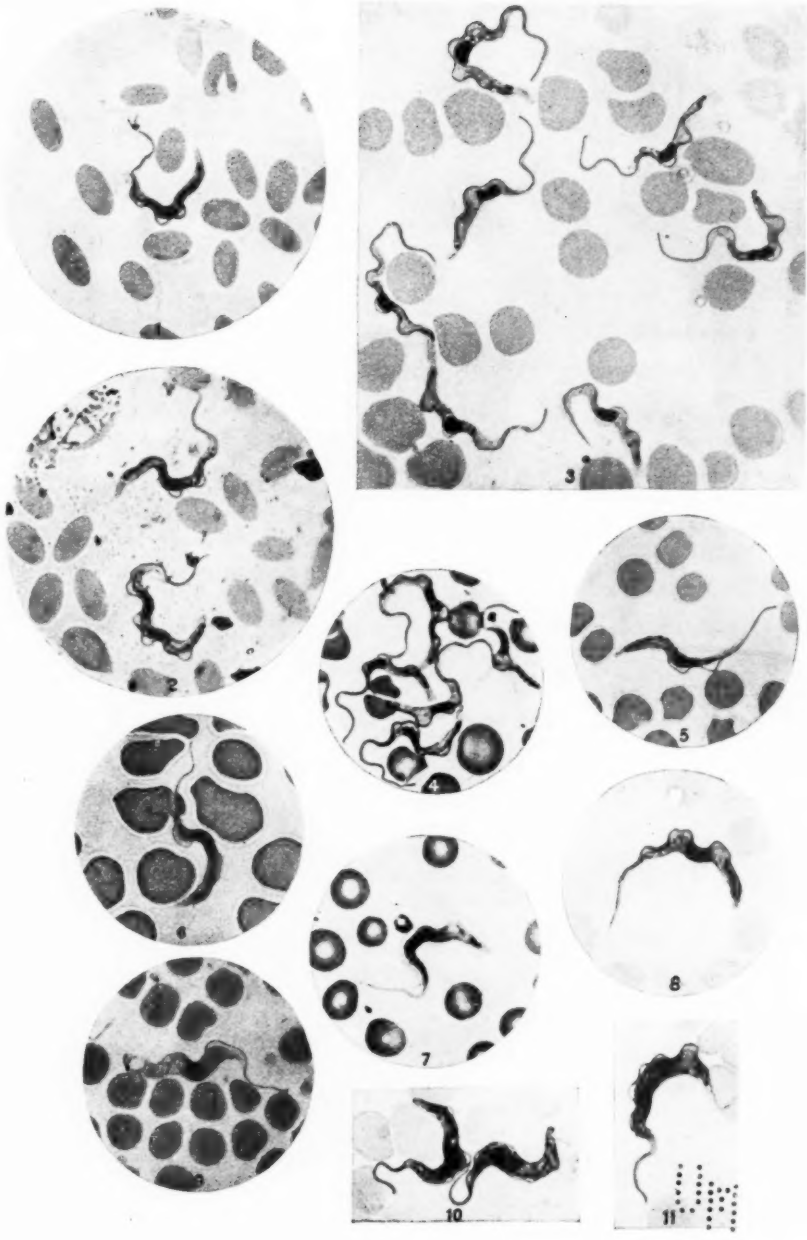
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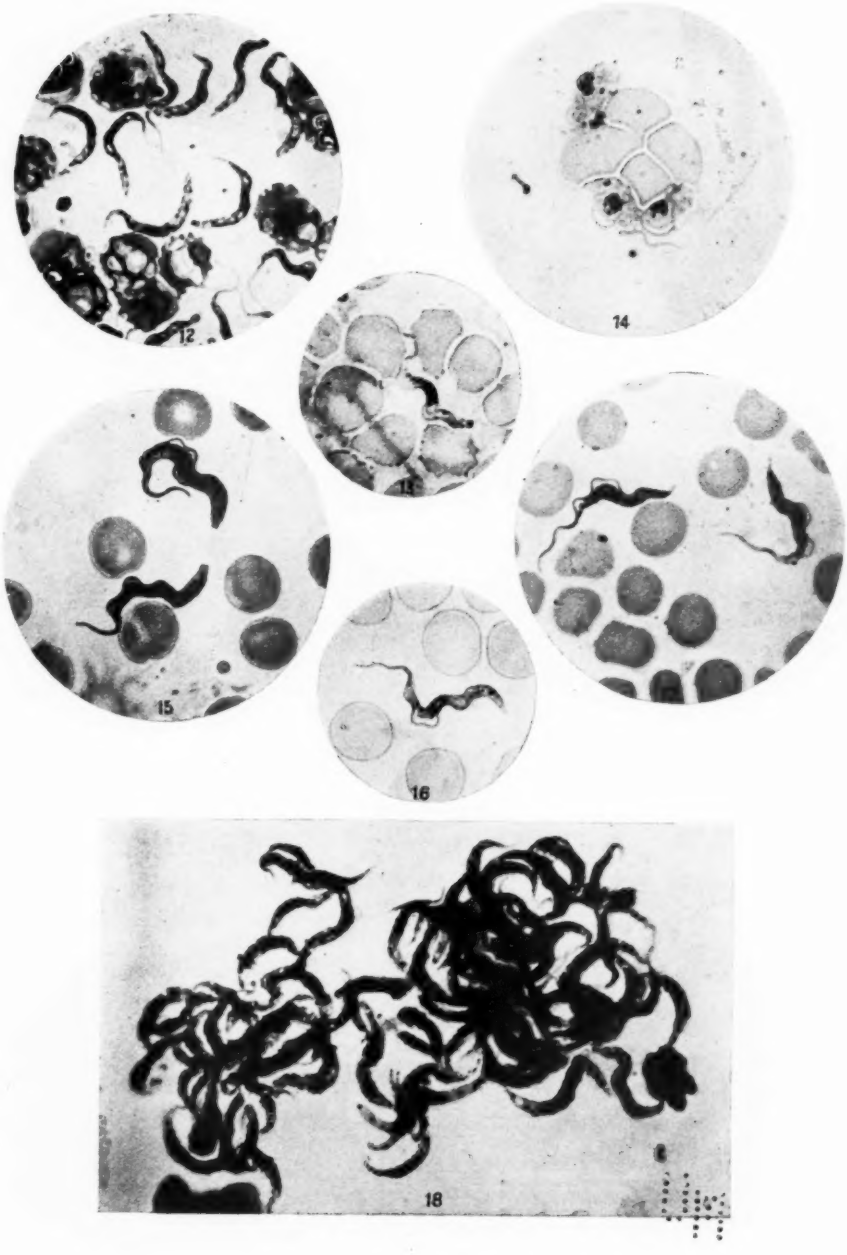
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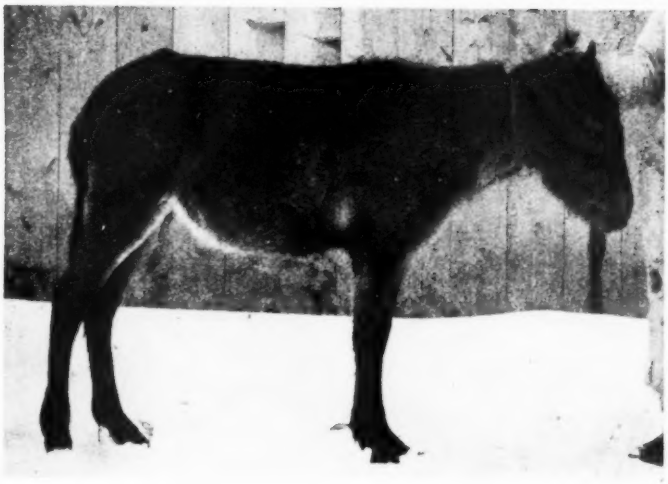

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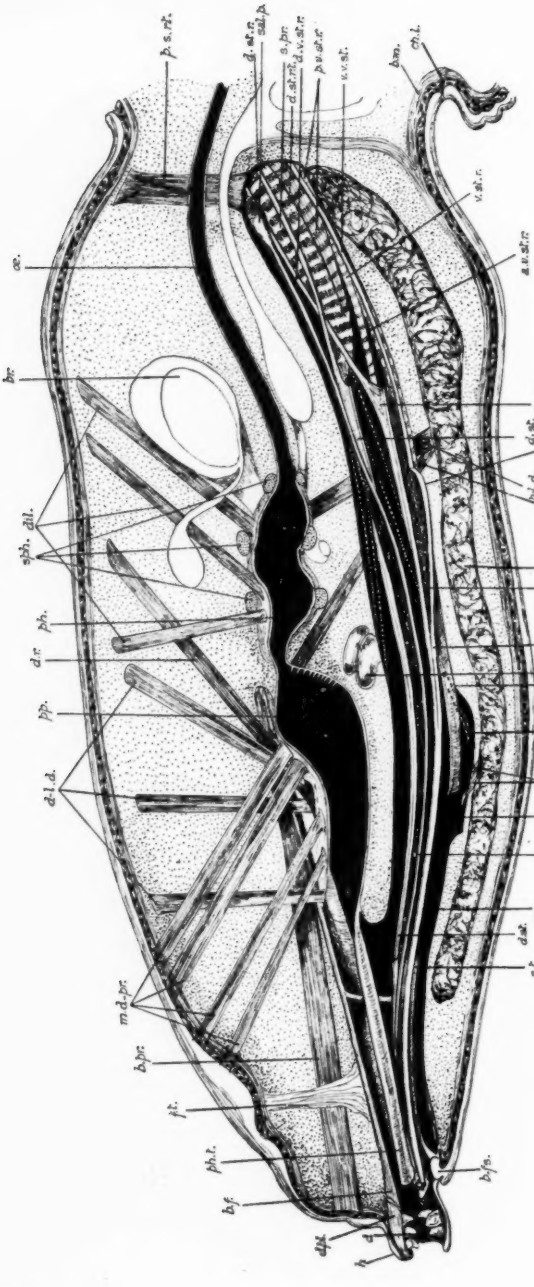
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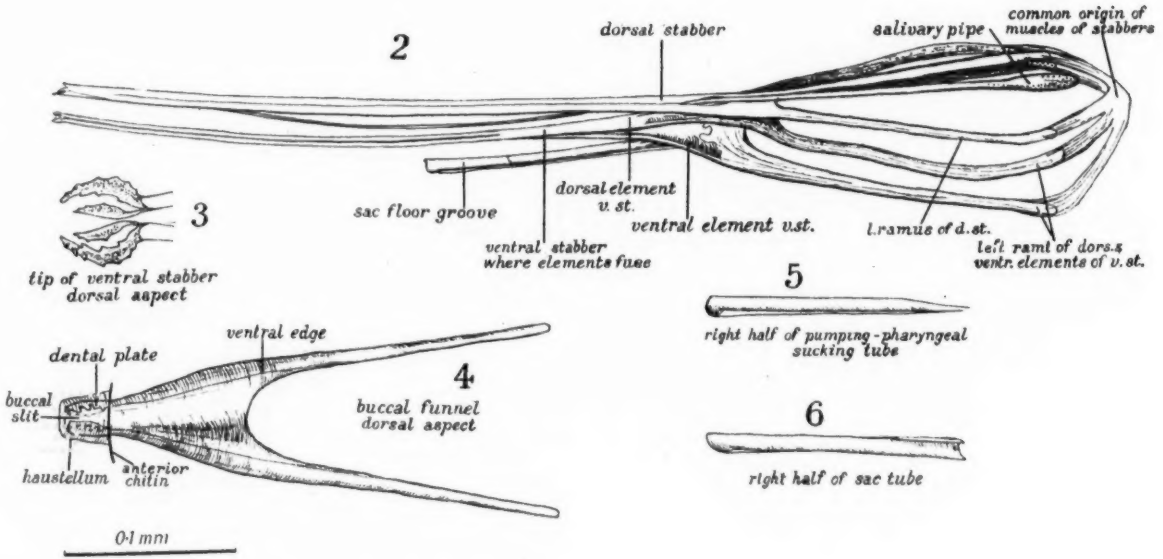
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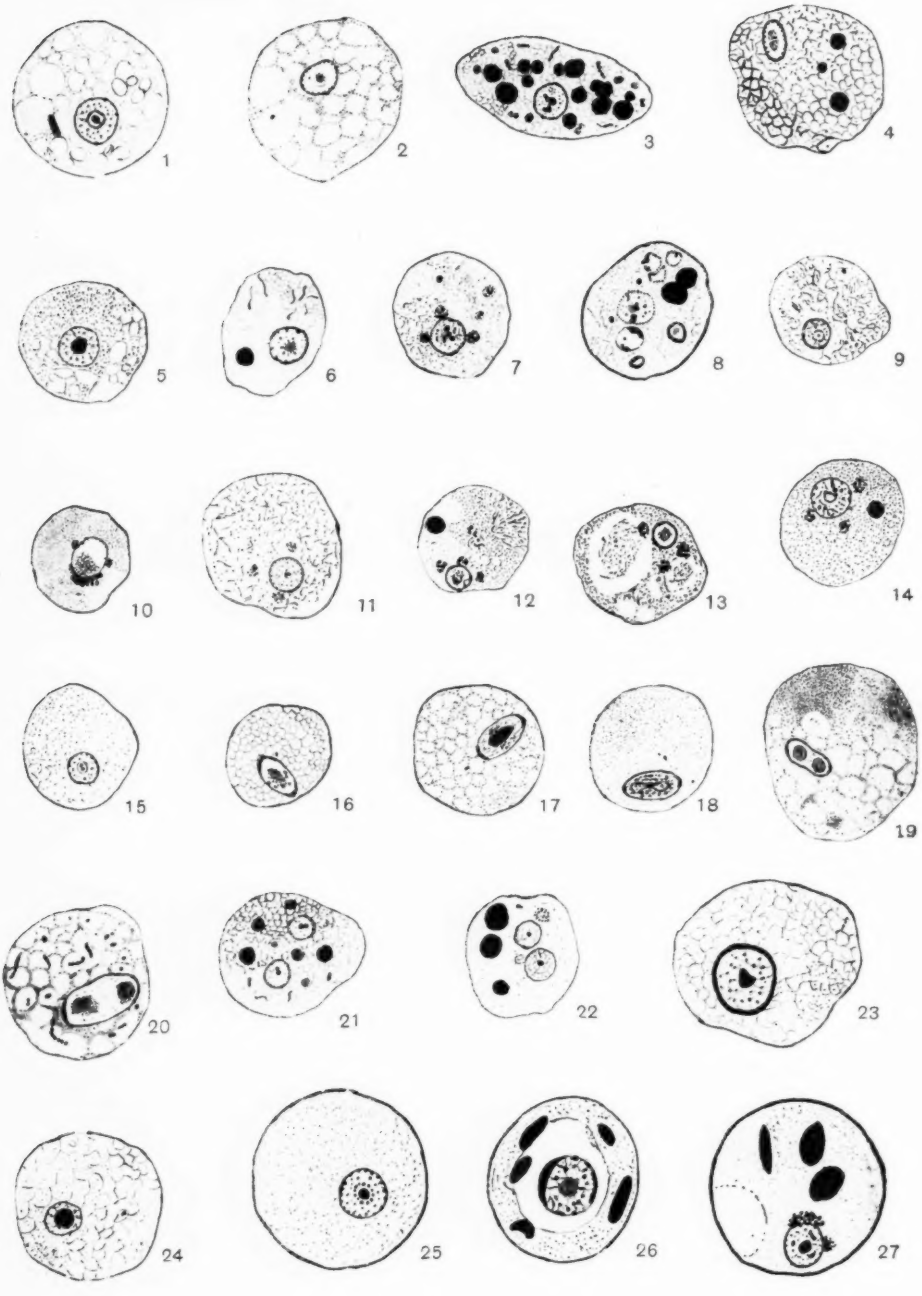
dorsal stabber
salivary pipe
common origin of muscles of stabbers
sac floor groove
dorsal element v. st.
ventral element v.st.
ventral stabber where elements fuse
l. ramus of d. st.
left rami of dors. & ventr. elements of v. st.
3
tip of ventral stabber dorsal aspect
5
right half of pumping-pharyngeal sucking tube
6
right half of sac tube
ventral edge
dental plate
buccal slit
4
buccal funnel dorsal aspect
haustellum
anterior chitin
0·1 mm

PLATE VI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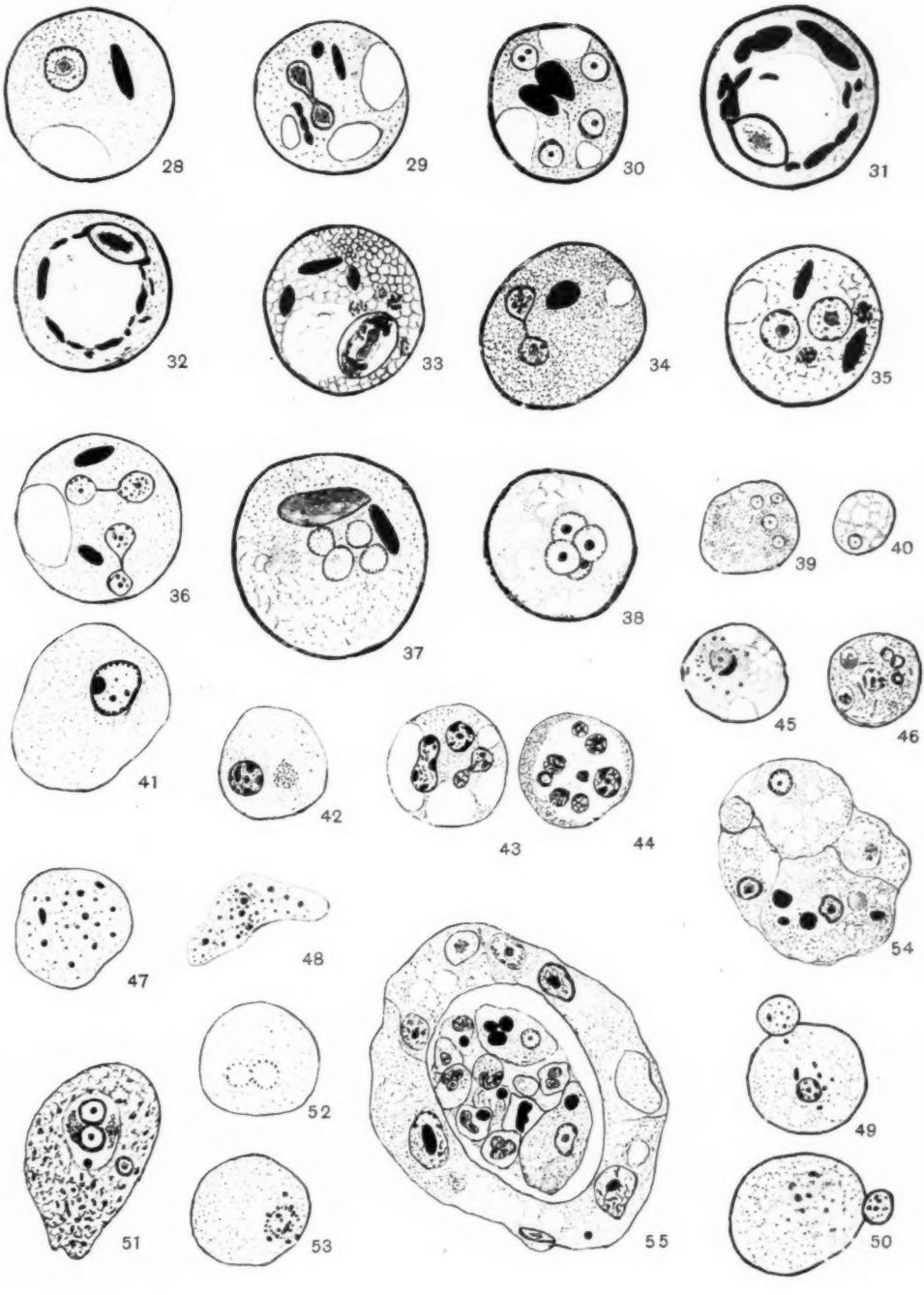
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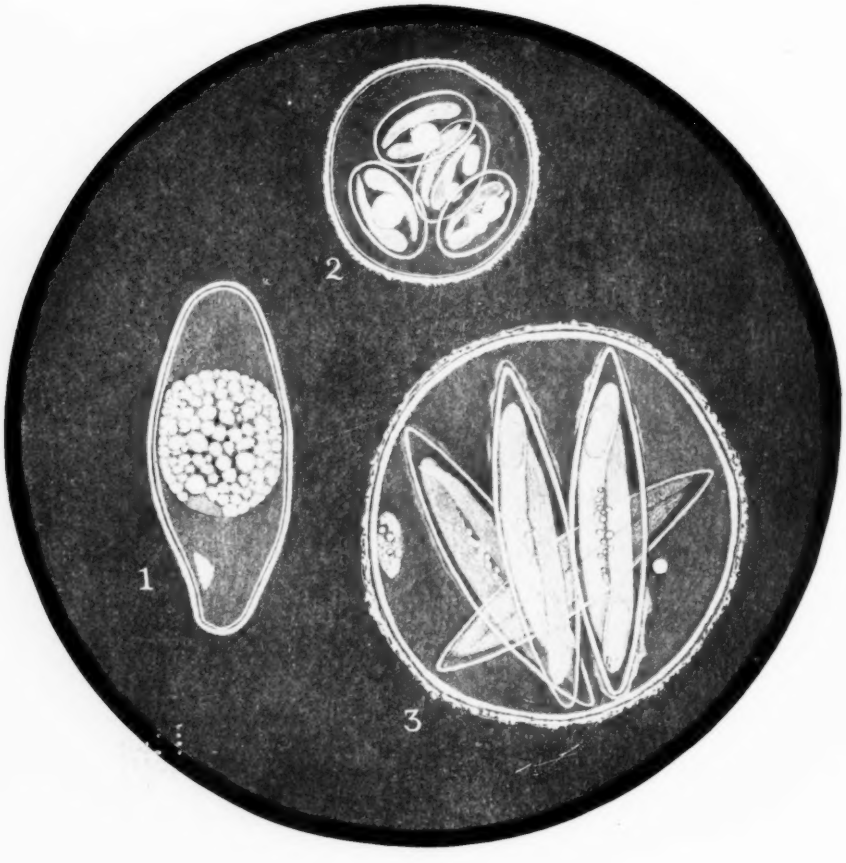

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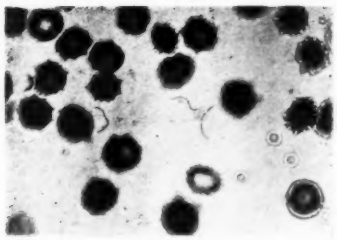
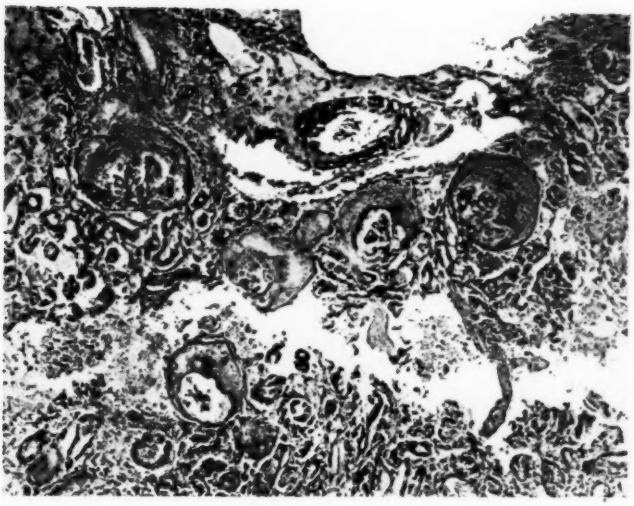
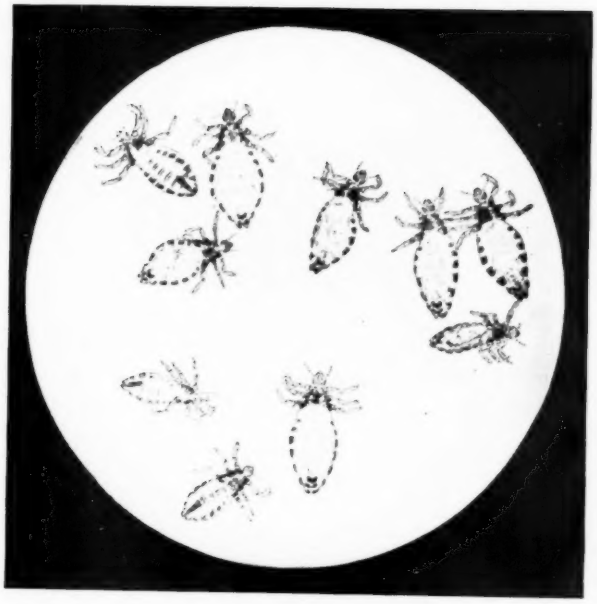
Coccidia of Man



Spirochaeta icterohaemorrhagiae. Guinea-pig, heart blood. × 640



Section of kidney of Guinea-pig. × 84



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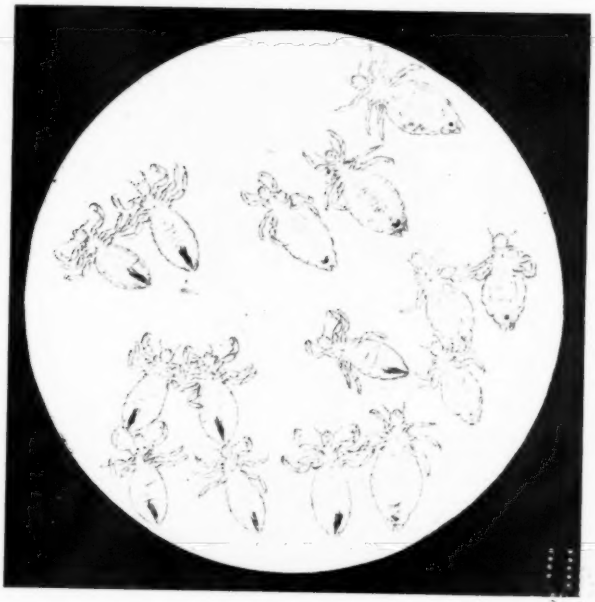

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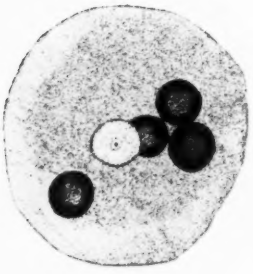

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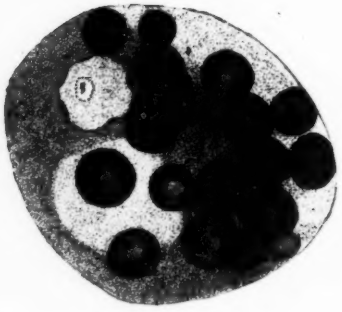
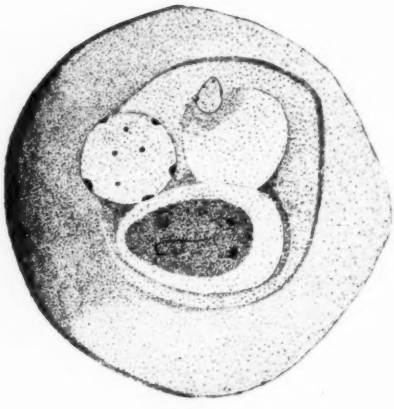


Fig. 2

Fig. 5



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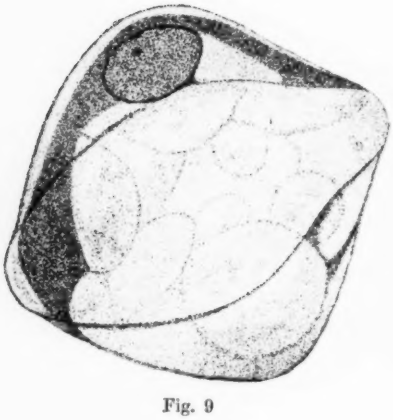

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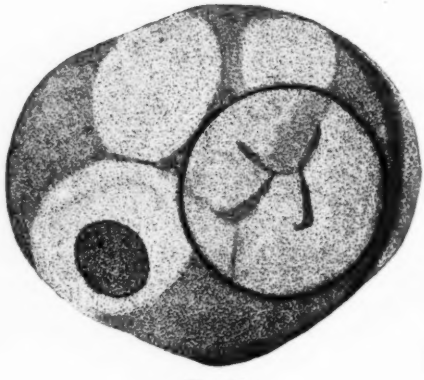

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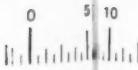

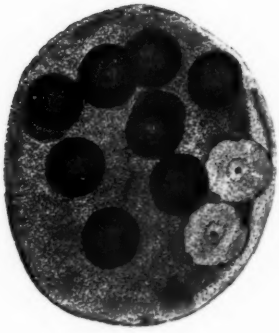

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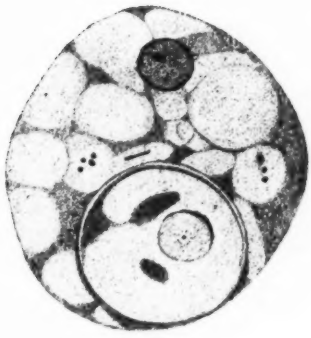

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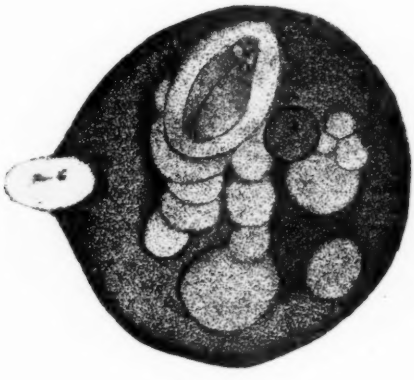

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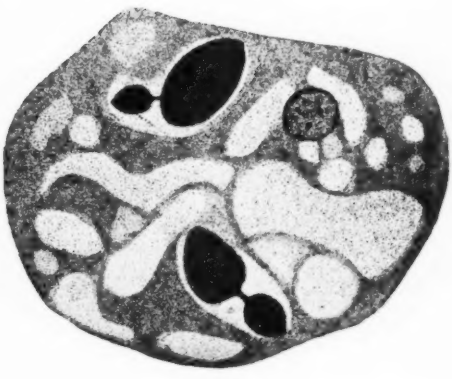

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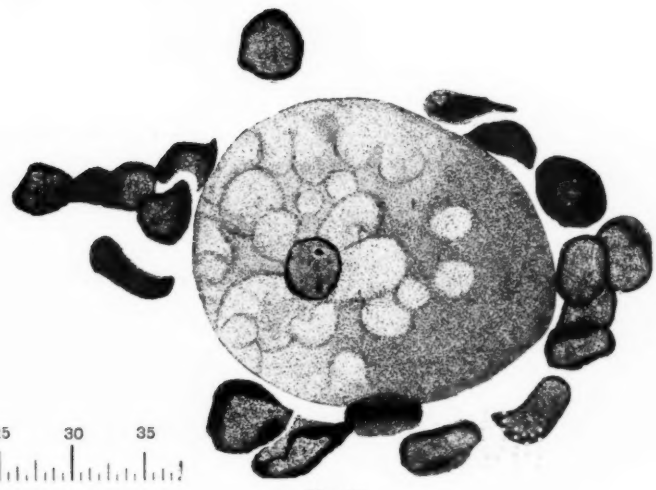
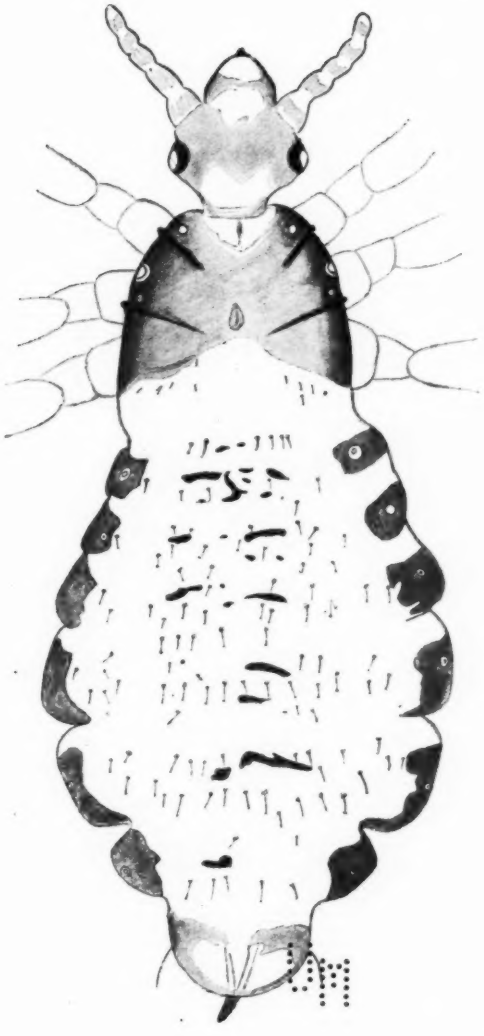


Scale in Microns.

5 10 15 20 25 30 35

Fig. 11



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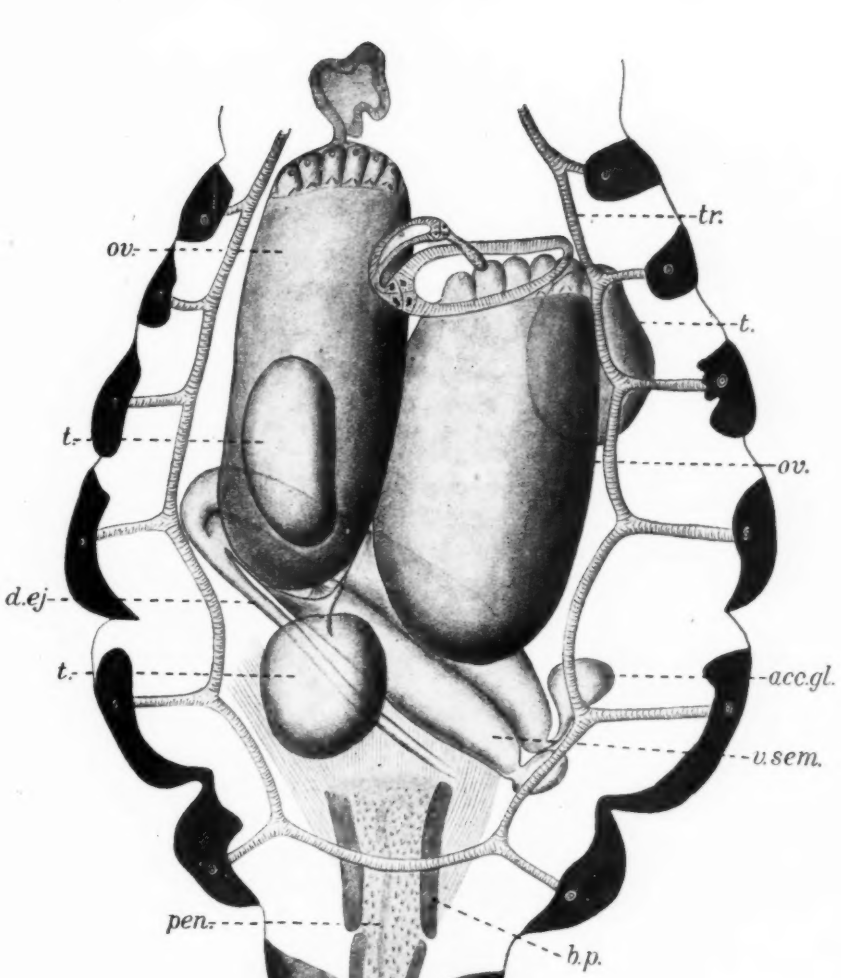

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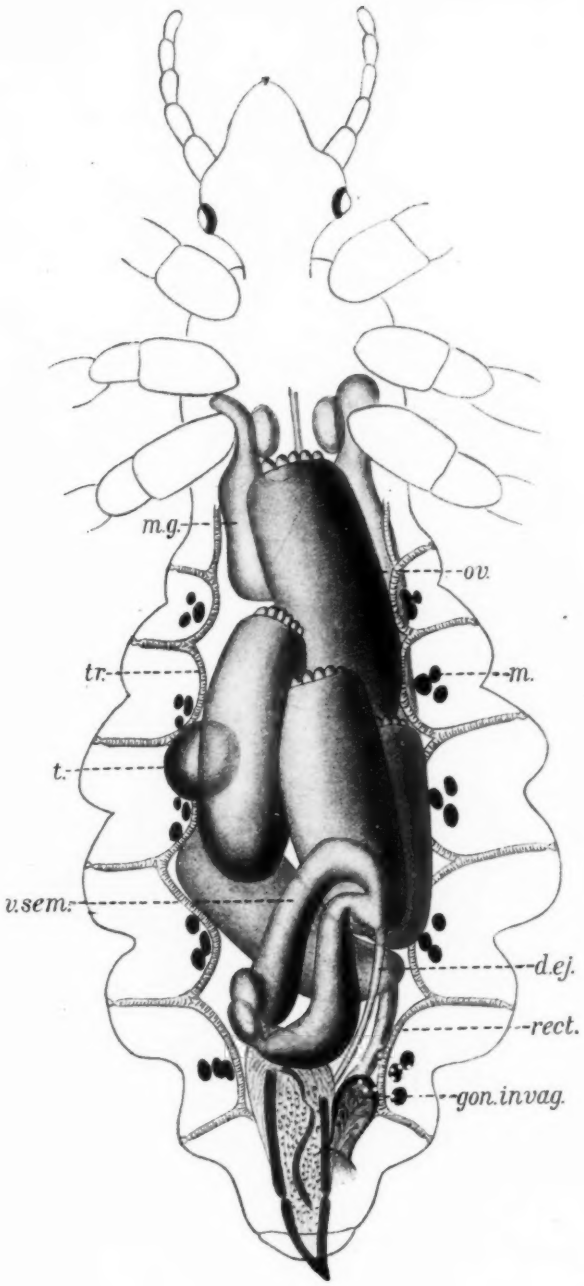

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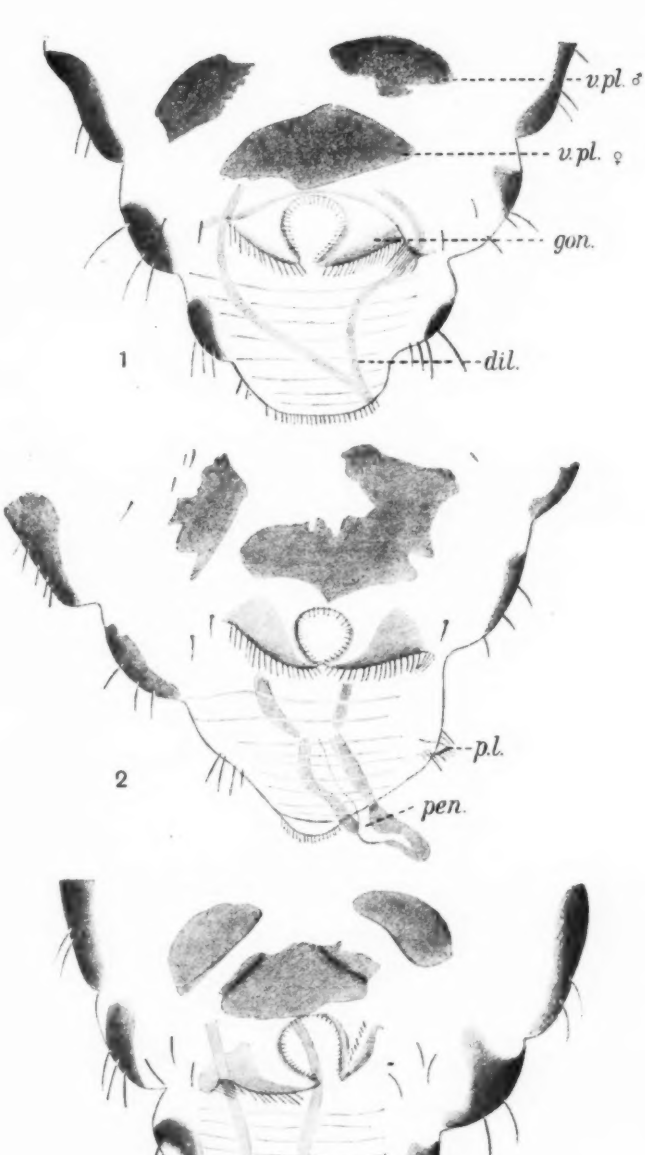

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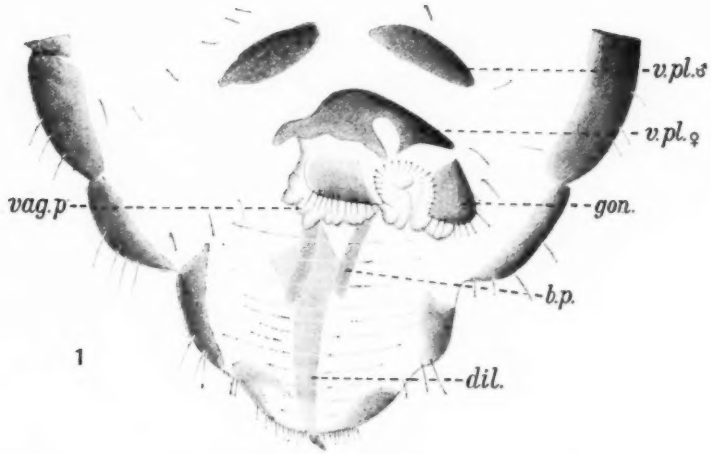

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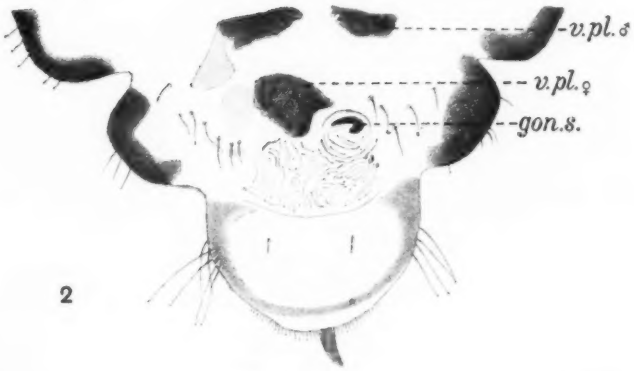

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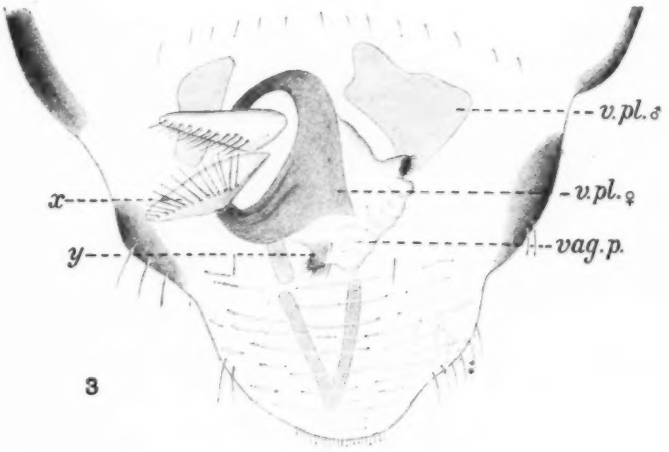

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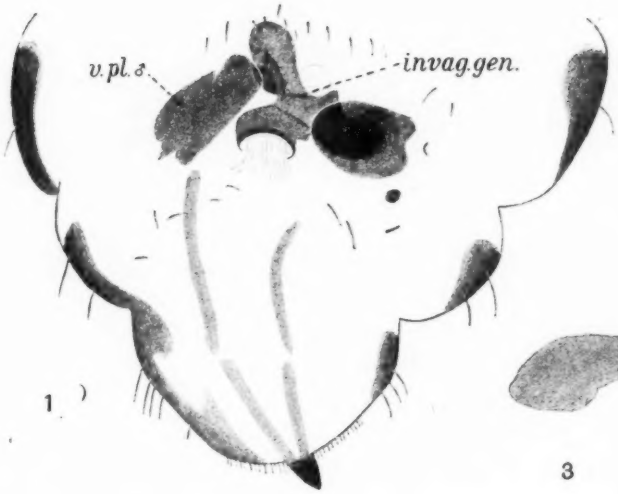

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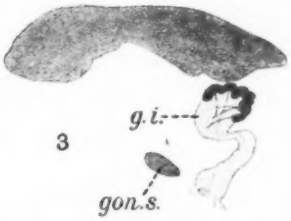

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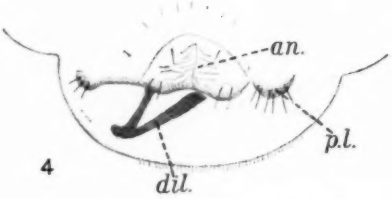

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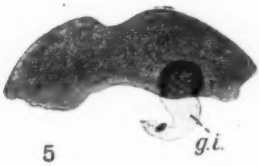

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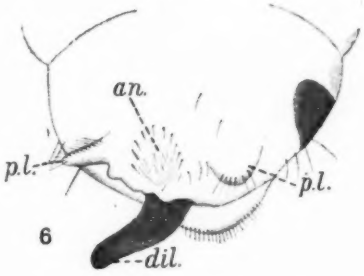

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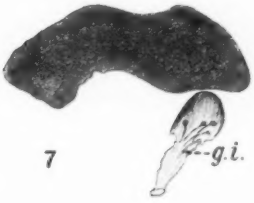

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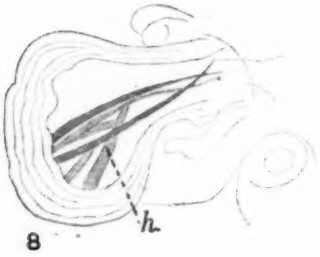

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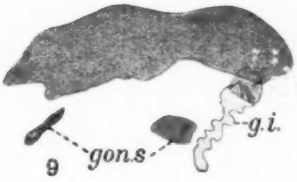

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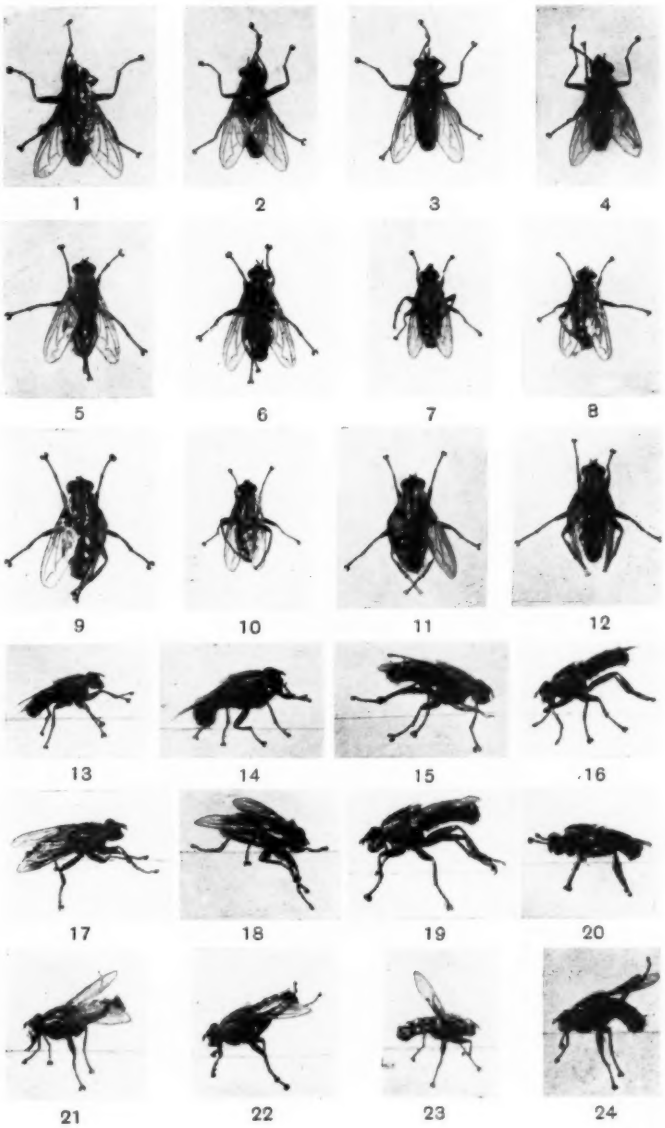
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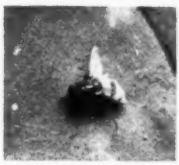

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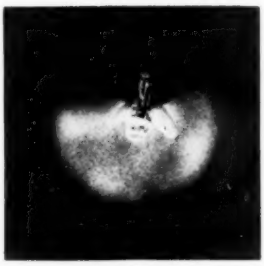

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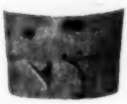

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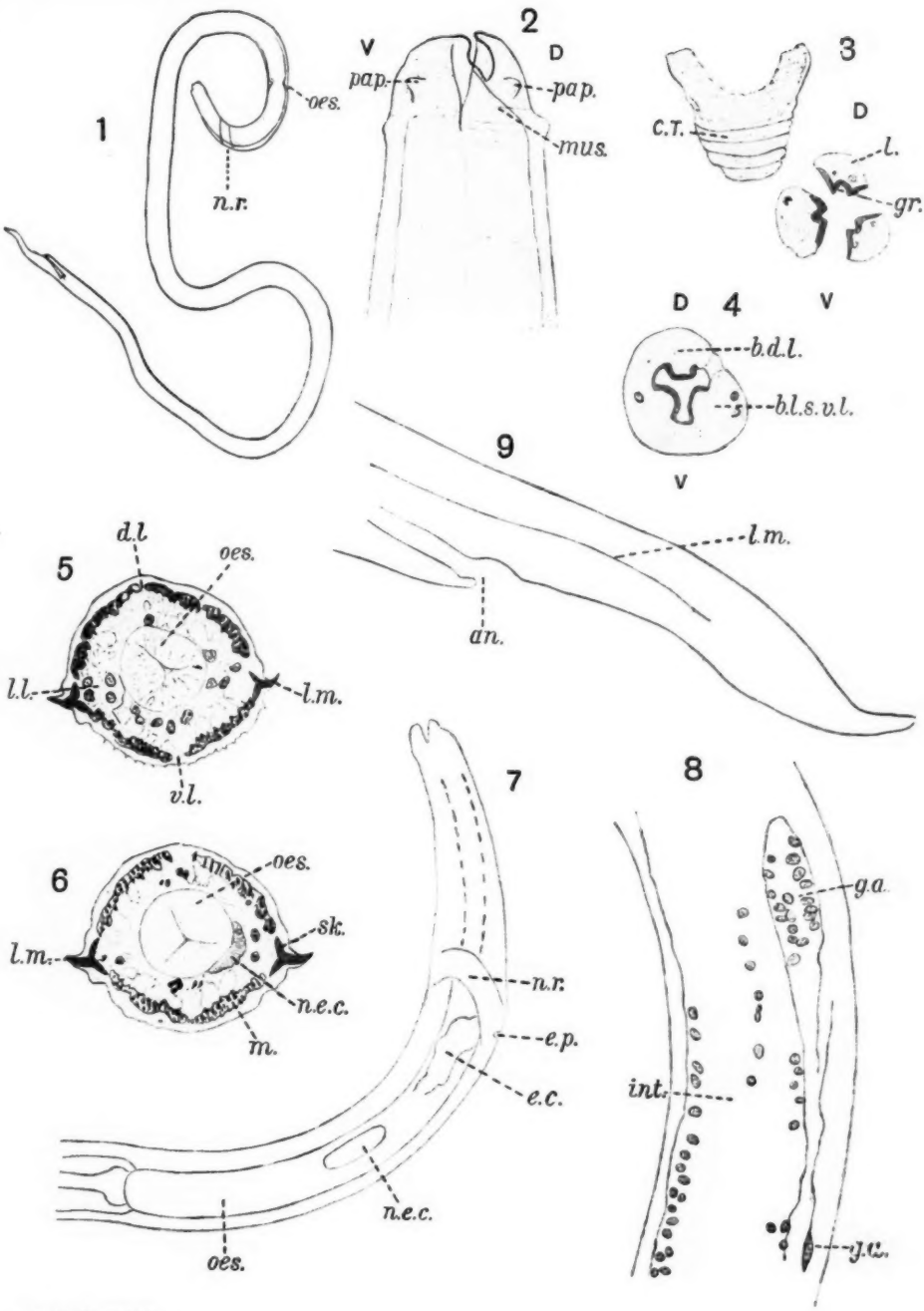

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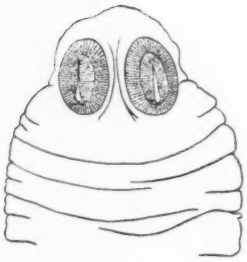

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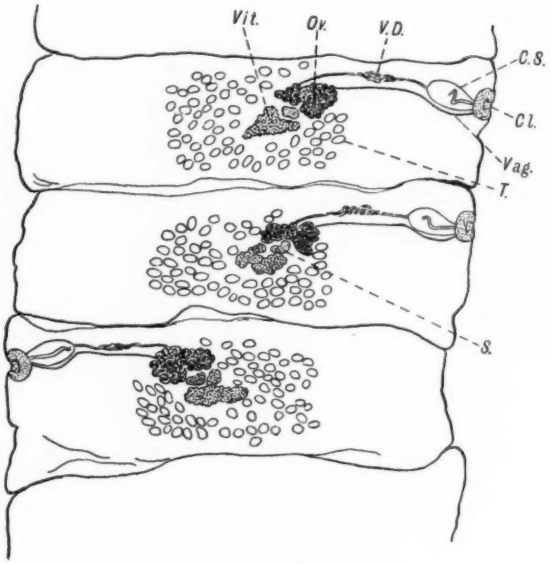

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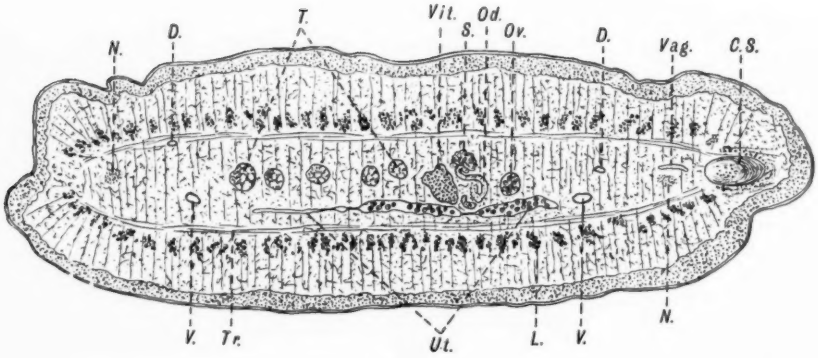


Fig. 3

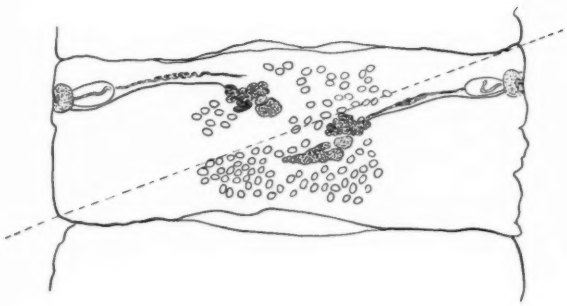


Fig. 4

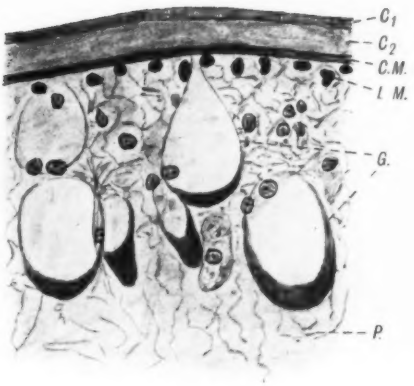
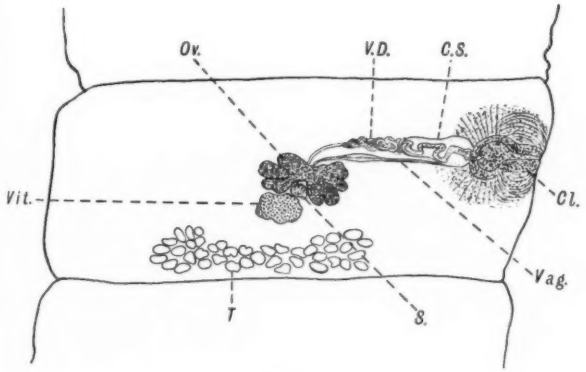


Fig. 5



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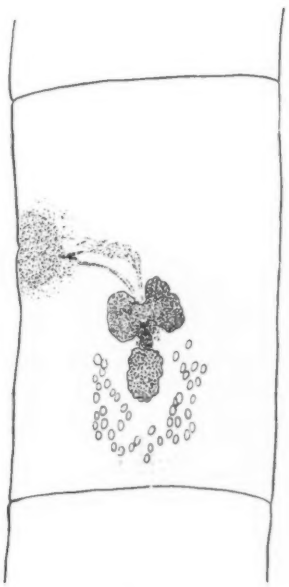

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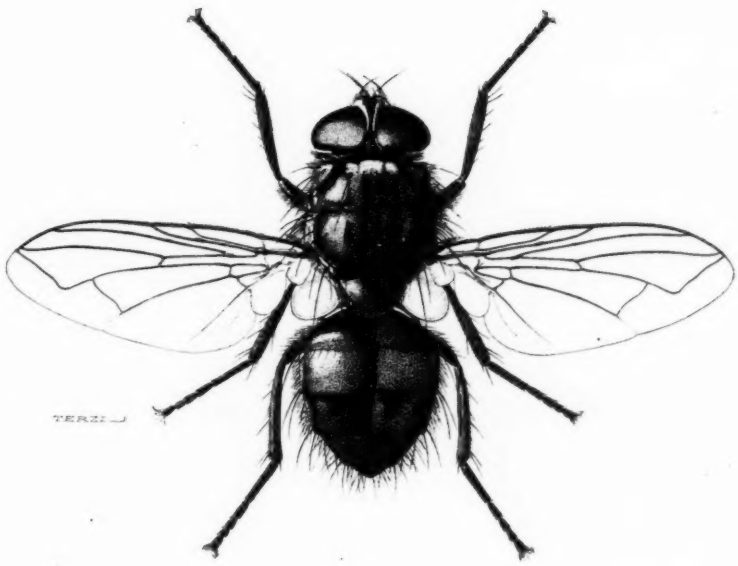

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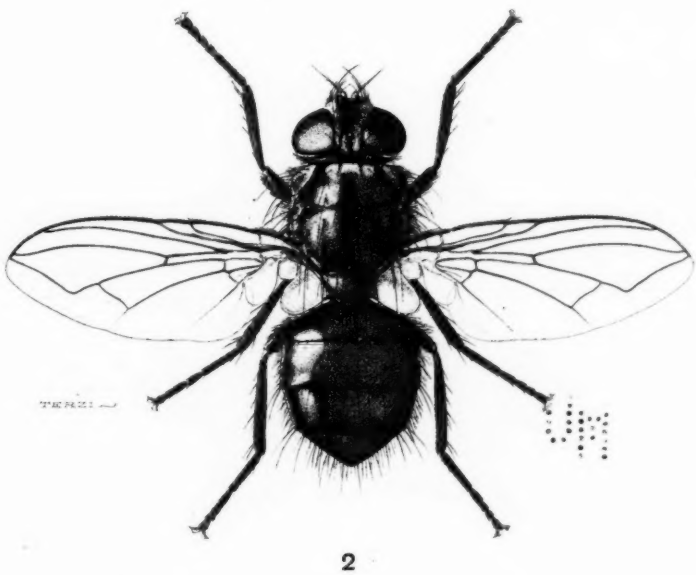

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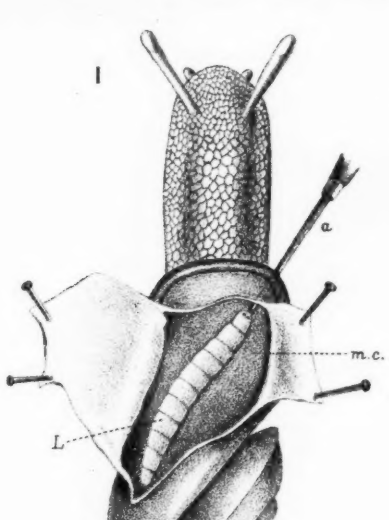
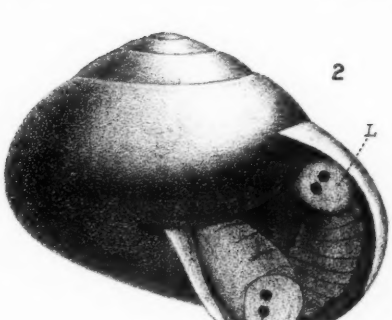
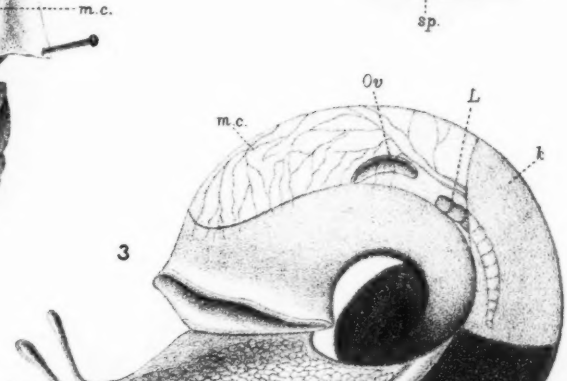
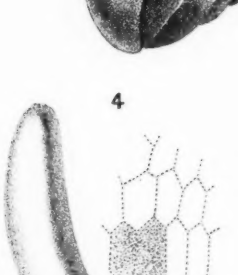
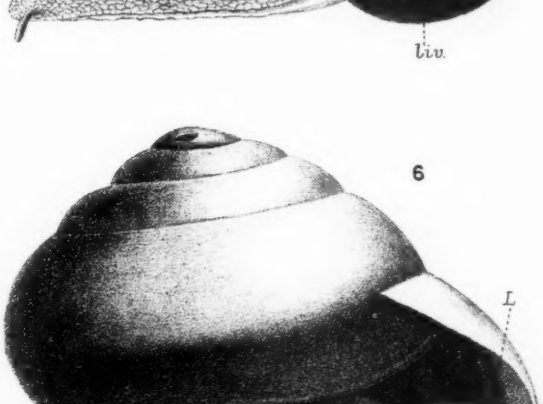
Melinda cognata Meigen, ♂ (1), ♀ (2)











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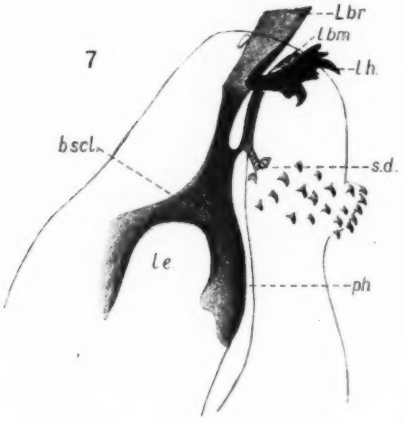
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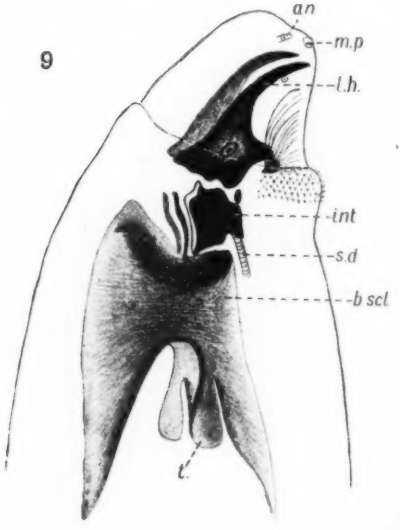
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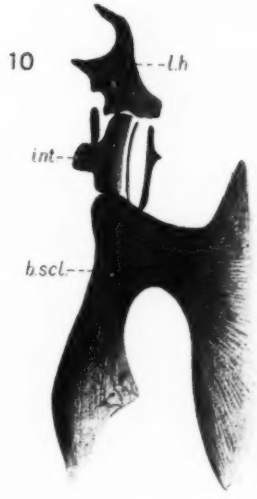
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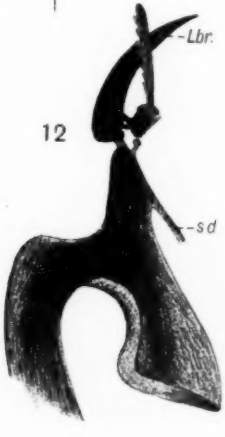
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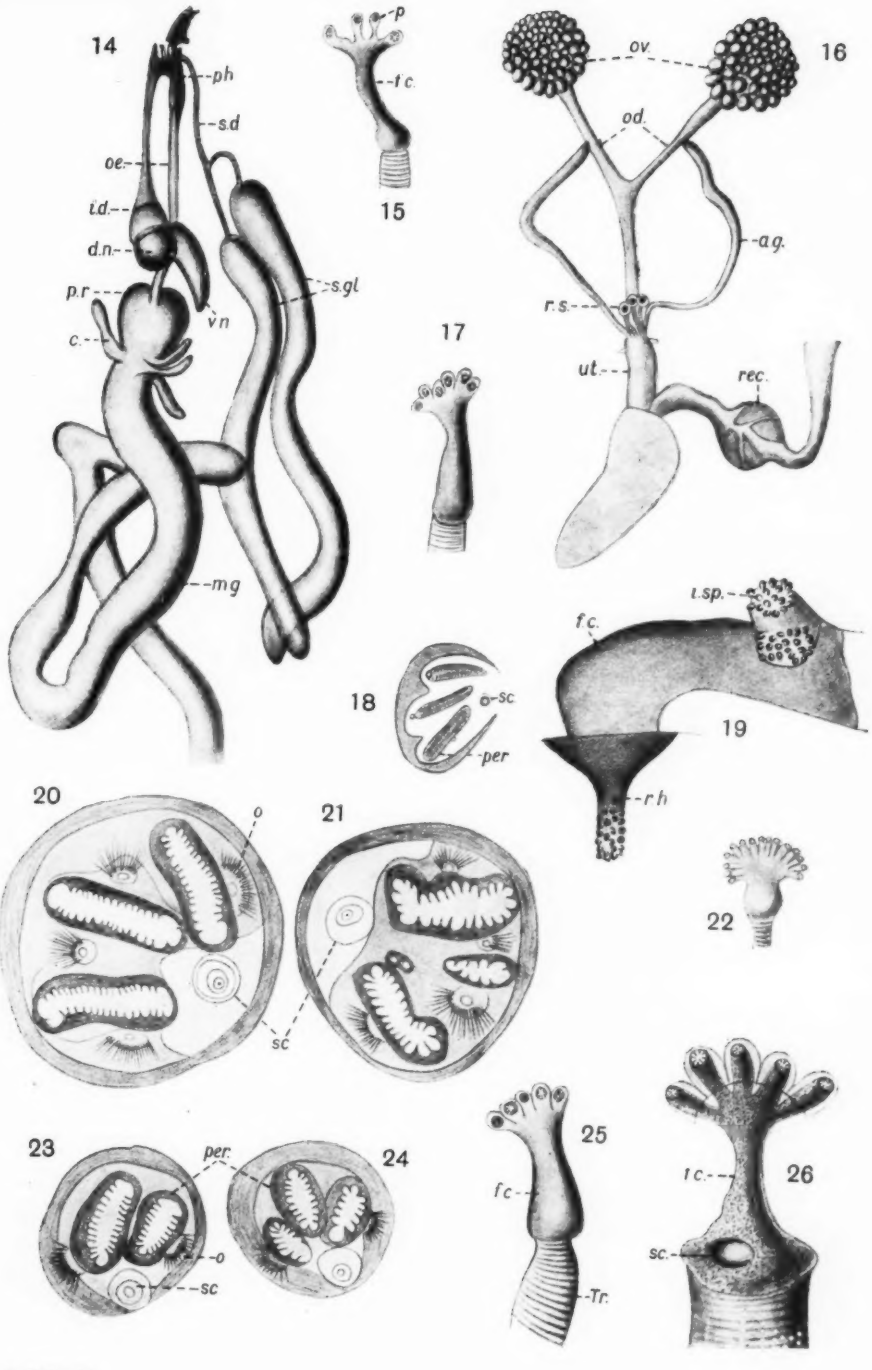
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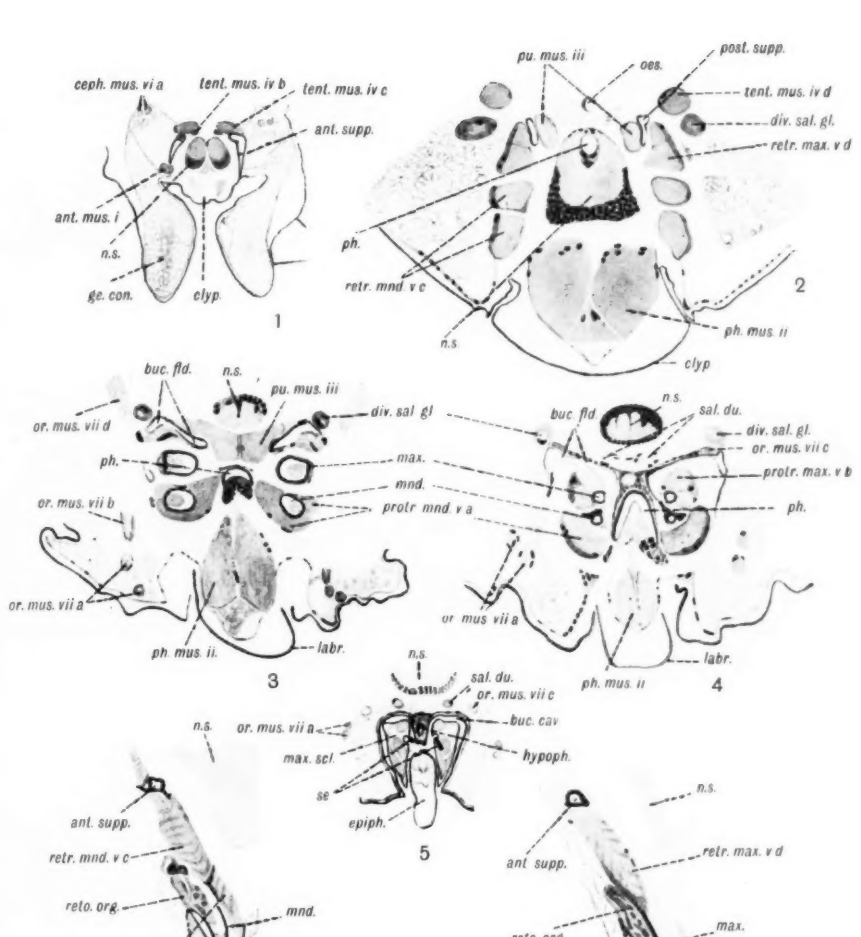
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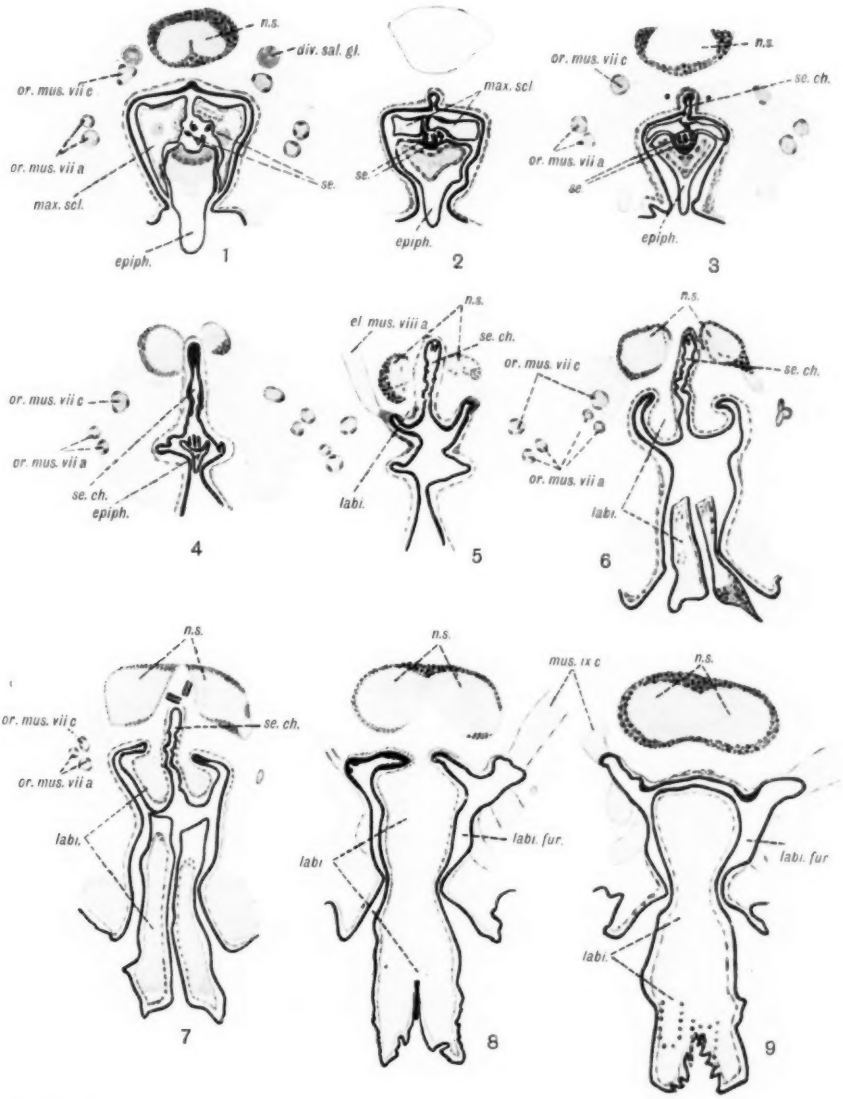
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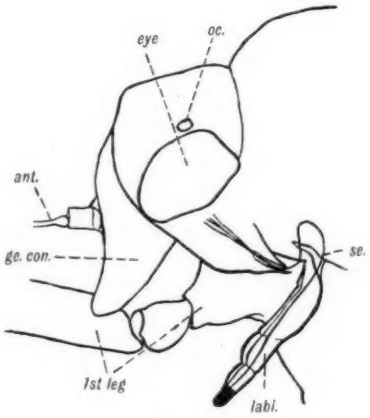

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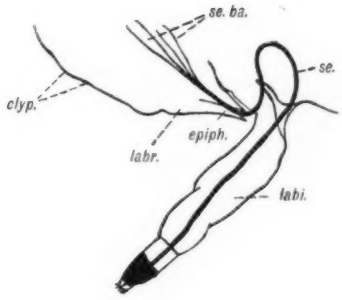

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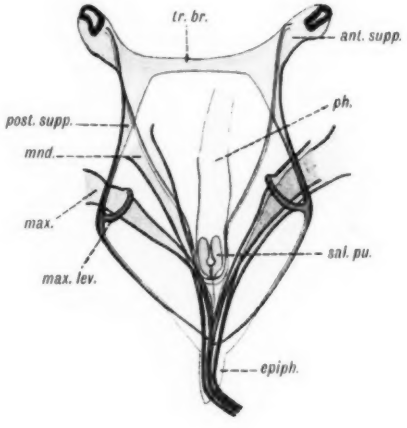

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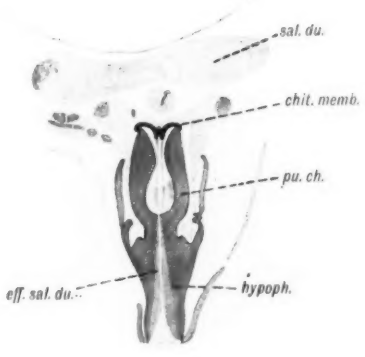

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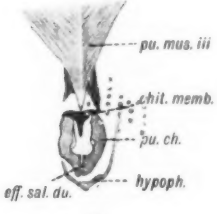

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